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THE DISTRIBUTION AND ECOLOGY OF THE CAVE SALAMANDER, *EURYCEA LUCIFUGA*

VICTOR H. HUTCHISON

Duke University, Durham, North Carolina

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INTRODUCTION

In recent years the ecology of salamanders has received the attention of many investigators. Hairston (1949) studied the local distribution and ecology of plethodontid salamanders in the Southern Appalachians. Gordon (1952) investigated the ecology and life history of the green salamander, *Aneides aeneus*. Hendrickson (1954) made an ecological and systematic study of the genus *Batrachoseps*. Bogert (1952) made field studies on the relative abundance, habits, and thermal levels of some Virginian salamanders.

Dunn (1926) greatly clarified the taxonomy and relationships of the family Plethodontidae. The genus *Eurycea* is one of the more advanced genera of this family, and *Eurycea lucifuga* Rafinesque, the cave salamander, appears to be one of the more advanced species in the genus. This salamander is widespread over much of the east-central United States, where it is most often found in the twilight zone of caves. (The twilight zone is defined as the area within a cave from the mouth to the point at which light is not detectable.) Banta & McAtee (1906) were the first to make an extensive study of this animal, but their paper dealt only with habits and life history. Ives (1951) visited one cave in Tennessee every month for a year and noted the changes in the visible population of this species. Other than these two papers, only occasional notes on the life history and distribution of the cave salamander have appeared in the literature. Notes on the habits, life histories, morphological and taxonomic relationships, and a discussion of the ranges of *Eurycea lucifuga* and *Eurycea longicauda* have been published (Hutchison 1956b). Since little is known about the ecology of this animal, the present study was undertaken to add to the knowledge of this species in particular and of the environmental conditions of the twilight zone of caves in general.

Unless stated otherwise, all references to *Eurycea longicauda* in this paper are to the nominate subspecies.

Assistance in the field was given by Dr. Richard G. Zweifel and the late Mr. Jon Phillips. Mr. L. L. Lucas and Mr. O. B. Williams granted permission to use caves on their property as study sites. The Virginia Polytechnic Institute Cave Club allowed me use of their files for help in locating caves. For helpful suggestions, lists of specimens, or loan of specimens, the author is indebted to the following persons and institutions: Arthur Loveridge, Museum of Comparative Zoology; Richard G. Zweifel, American Museum of Natural History; Doris M. Chochran, United States National Museum; William E. Duellman, University of Michigan Museum of Zoology; Neill D. Richmond, Carnegie Museum; Albert Schwartz, Charleston Museum; H. K. Gloyd, Chicago Academy of Sciences; James A. Fowler, The Academy of Natural Sciences of Philadelphia; Hobart M. Smith, University of Illinois Museum of Natural History; Robert F. Inger, Chicago Natural History Museum; Arnold B. Grobman, Florida State Museum; Herndon G. Dowling, University of Arkansas; Albert P. Blair, University of Tulsa; Ralph Sinclair; Sherman A. Minton, Jr.; and Paul Anderson. Grateful acknowledgment is also made to the Mountain Lake Biological Station and to the National Science Foundation for making the field work possible during the summer of 1955 through a grant-in-aid. Special thanks are accorded Dr. I. E. Gray and Dr. J. R. Bailey, Department of Zoology, Duke University, for their advice throughout the study.

PROCEDURES

This study consists of three parts: (1) a summary and discussion of the distribution of *Eurycea lucifuga*, (2) a field study through one year in Giles

County, Virginia, of the population dynamics, environmental factors, local distribution, possible competition with other species, and (3) experimental laboratory work on activity, critical thermal maxima, reactions to light, and vital limits of water loss of *E. lucifuga* and its closest relative, *E. longicauda longicauda*.

DISTRIBUTION AND HABITAT SELECTION

Published locality records, museum specimens, specimens in personal collections, and correspondence with several persons who have collected *Eurycea* were used to obtain as complete a picture of the distribution of this species as possible (Fig. 1). Where more than one record exists for a single county, generally only one dot is shown. *E. lucifuga* ranges from Tippecanoe County, Indiana, in the north, to Polk County, Georgia, in the south, to Mayes County, Oklahoma, in the west, and Rockbridge County, Virginia, in the east. This range falls within the Carolinian Biotic Province of Dice (1943).

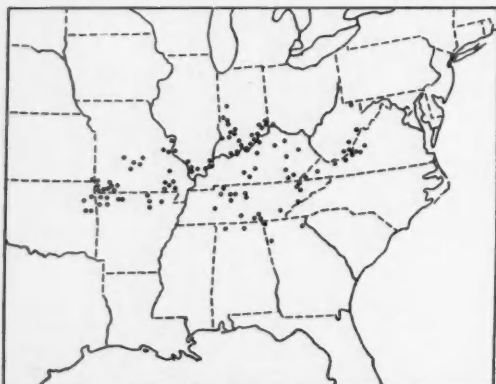


FIG. 1. The geographic distribution of *Eurycea lucifuga*. Each dot represents a county record based on museum specimens and literature records.

The great majority of the locality records for this salamander is from the twilight zone of caves. It is not a true troglobite (*sensu* Jeannel 1927), however, since it does not lack pigment or eyes and is in no apparent way modified for existence in a subterranean habitat. Eigenmann (1900) said of this animal, "There is nothing about the structure of the salamander that marks it as a cave species, but its habits are conclusive." Banta & McAtee (1906) report individuals from the deeper recesses of Mayfield's Cave in Indiana, where they had retreated, presumably to lay their eggs. Specimens reported from very deep parts of caves, such as that mentioned by Banta & McAtee from a spot 1.5 miles within Wyandotte Cave, were probably transported there accidentally, by high water, or possibly, through some small sink-hole connecting with the cave from the surface.

Several authors report specimens from beneath logs or stones or along streams issuing from limestone rock (Hay in Banta & McAtee 1906, Blatchley 1897,

Hutchison 1956a, and others). These records indicate that *lucifuga* is somewhat independent of caves in certain areas. With only one exception, however, every specimen reported was collected in a limestone area, as determined from geological maps such as those contained in a publication edited by Eckel (1913). Two questions arise from this correlation: (1) is the species limited to limestone? and (2) if it is not limited to limestone, why does it occur so much more often on limestone than on other substrates?

From observations on local distribution and from the locality records it appears that the species is not limited to limestone. This is supported by preliminary experimental work in the laboratory. The floor of a box 30 inches long, 12 inches wide, and 6 inches high was divided into two equal sections. Soil (pH6) was mixed with wet moss and placed in one section, and wet crushed limestone was placed in the other. The top was covered with a wire screen lid. Forty-three *lucifuga* were placed in this box singly and their position recorded after they were in the box one hour or more. Twenty were counted on limestone and 23 on the slightly acidic soil. A somewhat similar experiment was made on captive *E. multiplicata* by Bragg (1955). When these salamanders were presented with a choice of peat moss and limestone loam in a terrarium with a layer of sand in the bottom, they showed a decided preference for the limestone, and in "several days all were found dead and thoroughly dried out on this ball of now dry earth." But, as pointed out by Bragg, reluctance to leave the limestone ball may have been due to an aversion to crossing the sand rather than to an active preference for the limestone. He also states that *lucifuga* in Cherokee County, Oklahoma, is "common at larger springs, especially in creek valleys, where it hides in the wet moss and other vegetation"; whereas *E. longicauda melanopleura* is "common in caves." This is the opposite of observations made by the author in western Virginia, but different environmental conditions in the two areas undoubtedly exist, and the two species apparently do not show the same tendencies toward inhabiting caves throughout their range. Also, different races of *longicauda* occur in the two areas.

In answer to the second question the author can only offer a hypothesis. Almost all caves of any appreciable size within the range of *lucifuga* are in limestone, a substrate that is most likely to possess caves and deep crevices due to a high solubility. It is in the twilight zone of such caves that *lucifuga* finds an optimum environment. The species would probably also be abundant on any other substrate within its range which would produce very similar ecological conditions.

Vernberg (1955) studied the reactions of *Plethodon cinereus* and *P. glutinosus* to soil pH in the laboratory and in the field. He found that in the laboratory experiments both species preferred a soil pH of 6.3 to 5.8, but in the field both species occurred in a wide range of soil pH. From these experiments and from observations of others, one must conclude that

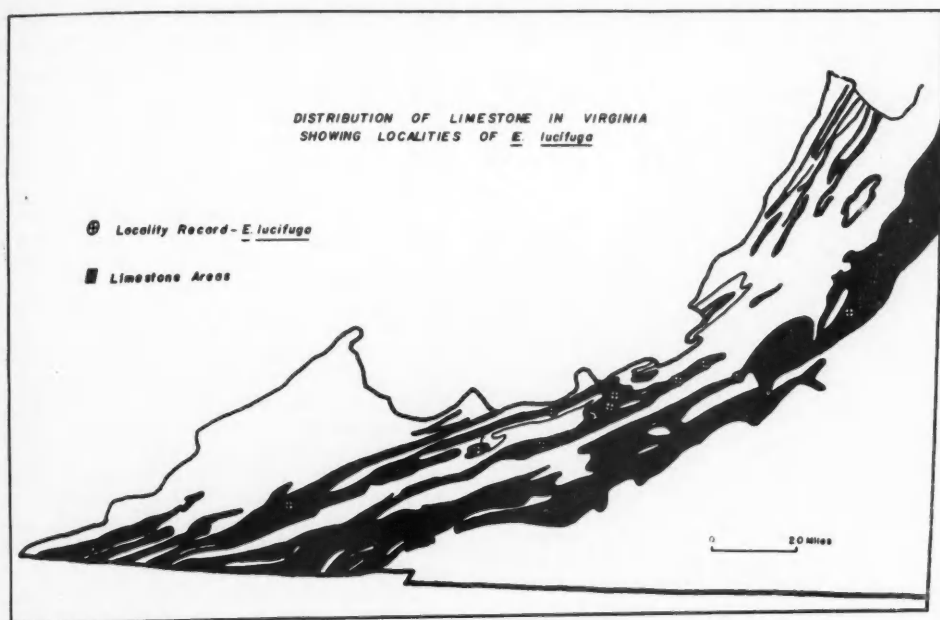


FIG. 2. The distribution of *Eurycea lucifuga* correlated with the distribution of limestone in Virginia.

pH *per se* has little to do with distribution but that pH is closely correlated with other variable environmental factors. In the case of *lucifuga*, it is the habitat of caves, crevices, and other solution features characteristic of limestone, and not the alkalinity of the substrate, which determines distribution.

The striking exception to this correlation of distribution with limestone deserves mention. Two specimens of *lucifuga* (USNM 115620-1) were collected by Dr. J. M. Valentine at Demorest, Habersham County, in northeast Georgia, in the center of a large area of crystalline rock, far removed from any limestone area. The nearest recorded locality for the salamander is in northwest Georgia, approximately 100 miles distant. These two specimens have been examined and were found to be correctly identified, and the locality record has been verified.

Figure 2 shows the known distribution of *lucifuga* correlated with limestone in Virginia. One can readily see from this map that every record is from an area of limestone. Fowler (1944) summarized the distribution of this species in Virginia and discussed its distribution in relation to drainage systems. There appears to be no correlation of distribution with watersheds. Further collecting in western Virginia will undoubtedly reveal numerous other localities for this species, since caves are very numerous in this area. *E. lucifuga* is apparently absent from certain areas in the state, however, and there is no readily understandable reason. For example, the author and several other collectors have visited caves extensively in Montgomery County, where environmental conditions appear to be nearly the same as those in caves in

neighboring Giles County, 15-30 miles away, but no *lucifuga* were found. The long-tailed salamander, *E. longicauda*, is prevalent in this area. *Plethodon wehrlei* is also common in many of the caves in Montgomery County.

It thus appears that *E. lucifuga* is found on limestone because this rock, due to its high solubility, is most likely to produce caves and it is the ecological conditions of the twilight zone of these caves and not any chemical properties of the rock *per se* which have attracted the species. The Habersham County, Georgia, locality record indicates the species is also likely to occur in crystalline rock areas where ecological conditions are favorable. Small caves are sometimes found in crystalline rock due to factors other than solution. Such small caves occur in Habersham County (Neill 1957), but are rare in such a substrate. A search of small caves in such areas in the Appalachians, particularly around the periphery of the mountains, may reveal additional records of this species. It has not been reported from North Carolina, but continued collecting in favorable habitats may reveal the presence of the species in the state.

FIELD STUDIES

DESCRIPTION OF THE STUDY AREA

The caves selected for study are located in the Appalachian Valley and Ridge Province (Fenneman 1938) in Giles County, Virginia, within a 3-mile radius of Newport (Fig. 3). This area has extensive limestone deposits with numerous caves, affording ample habitat for the cave salamander, which is locally abundant; the caves for this study occur in the

Stones River group of Ordovician limestone. The county has an average January temperature of 0°C and an average July temperature of 21.1°C . The area has an average annual precipitation of 38 inches, 20-22 in falling in the warm period from April to September (U. S. Dept. Agriculture 1941). A U. S. Weather Bureau rain gauge station is located 200 yds from the entrance of Tawney's Cave.

Three caves were selected as "controls" and are designated as A, B, and C in Fig. 3. Four additional caves were used as "study caves"; these are marked 1, 2, 3, and 4 in Fig. 3 and have the following exact locations: (1) Tawney's Cave (also known as Tony's or Torney's), Long $80^{\circ}30'45''\text{W}$ and Lat $37^{\circ}18'45''\text{N}$ at an elevation of approximately 1850 ft (564 m) on the lower south slope of John's Creek Mountain, 1.6 mi northwest of Newport; (2) Lucas Cave, Long $80^{\circ}28'57''\text{W}$ and Lat $37^{\circ}19'44''\text{N}$ at an elevation of approximately 2075 ft (640 m) on the west slope of Clover Hollow Mountain, 2.5 mi north-northeast of Newport; (3) Link Cave, Long $80^{\circ}32'10''\text{W}$ and Lat $37^{\circ}17'53''\text{N}$ at an elevation of approximately 2075 ft (633 m) on a small spur on the lower north slope of Spruce Run Mountain, 2.6 mi west-northwest of Newport; (4) Williams Cave, Long $80^{\circ}31'51''\text{W}$ and Lat $37^{\circ}17'53''\text{N}$ at an elevation of 1790 ft (546 m) on the south slope of John's Creek Mountain, 2.2 mi northwest of Newport.

ENVIRONMENTAL ANALYSIS

Methods

From about June 20 to August 23, each study cave was visited every three days; and monthly visits were

made every month thereafter, except during December and May. During the study period a number of physical factors were recorded: air temperature, saturation deficit, evaporation, light, precipitation, and air movement. Three stations were selected at each cave: Station 1, outside cave mouth; Station 2, within the twilight zone, at the approximate mid-point of the density of salamanders seen on the first visit; Station 3, at the approximate end of the twilight zone, where light from the entrance was not visible, or just barely so.

Air temperatures were taken with a Weston Model 226 dial thermometer, which was also found to be ideal for insertion into crevices, where the salamanders were most often found. During the summer period of the study, maximum-minimum temperatures were taken with Taylor Maximum and Minimum Registering Thermometers No. 5448. Continuous records were taken for a period of one week at Station 2 in each of the caves by means of a Friez hygrothermograph and Friez thermograph.

Saturation deficits were calculated by the use of a Baker Nomogram (Baker 1936) from readings taken with a Henson cog-type psychrometer.

Light was recorded with a Weston Model 603 Illumination Meter and a Weston Master II Exposure Meter. A conversion table giving foot-candles for the latter instrument was supplied by the manufacturer. The lower light values obtained at the dim end of the twilight zone were inaccurate, and the values obtained were only approximate.

Evaporation was recorded by means of Livingston

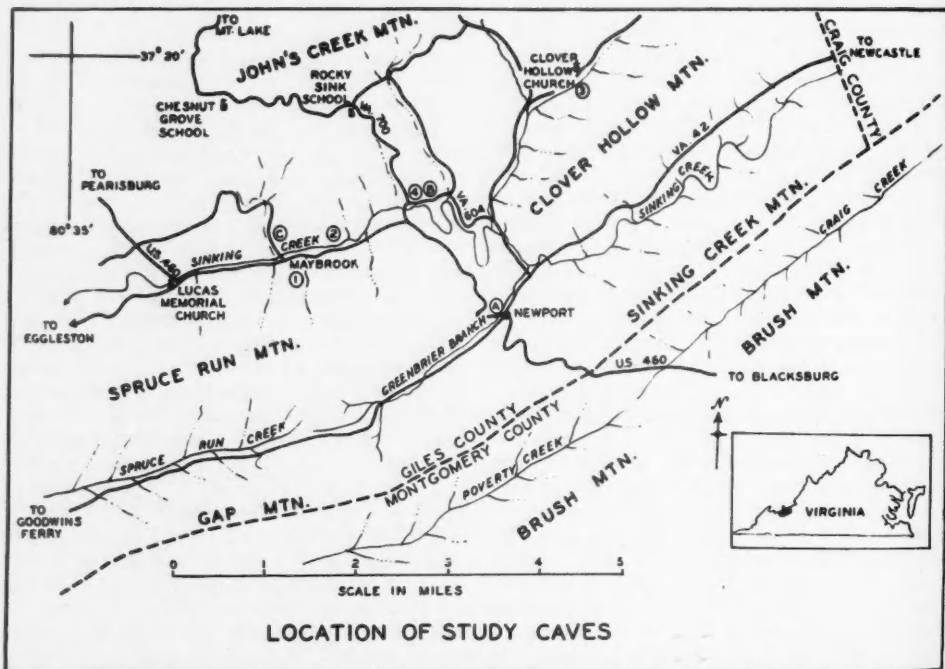


Fig. 3. Map of the study cave area. Numerals represent study caves; letters, control caves.

atmometers. A black and a white atmometer bulb were placed at each station during the summer months, and the total amount of evaporation from each bulb was recorded.

Precipitation data were obtained from the U. S. Weather Bureau Rain Gauge Station at Newport, Virginia, and from published weather data (U. S. Dept. Commerce 1955, 1956). This rain gauge is located within 2.5 miles of all the study caves.

Air movement was determined with a Taylor jeweled anemometer, Model No. 3132, provided with an improved vane and ball-joint swivel in order that air movement from any direction could be recorded.

TEMPERATURE

Fluctuations in temperature for the three stations at two study caves are shown in Fig. 4. These graphs are also representative of temperature conditions in the others study caves. The outside temperature fluctuated as much as 29°C over the study period, but the temperatures at Stations 2 and 3 showed much less variation. The following maxima and minima were recorded: Link Cave—Station 2, 14.6°C (July) and 5.5°C (March); Station 3, 10.7°C (September) and 8.8°C (April). Williams Cave—Station 2, 11.5°C (July) and 5.0°C (January); Station 3, 10.5°C (September) and 8.0°C (February). Lucas Cave—Station 2, 15.5°C (August) and 6°C (January); Station 3, 10.8°C (June, July) and 7.9°C (April). Tawney's Cave is unusual in having a large upper entrance and two smaller lower entrances and in having throughout the year a steady outflow of air at the lowest entrance, the location of Station 2. As a result temperatures at Stations 2 and 3 were almost identical; the difference in recorded temperature for these stations was never more than 0.5°C .

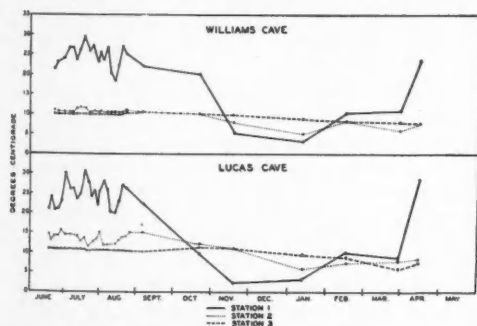


FIG. 4. Changes in temperature at Williams Cave and Lucas Cave from June, 1955, to April, 1956.

A temperature lag of a month or more is shown at Stations 2 and 3 after the outside temperature trend changes. This temperature lag increases with depth in the cave, resulting in the greatest temperature lag at Station 3. The degree of temperature change inside the cave is undoubtedly dependent on the size of the cave and of the cave openings to the surface. Link Cave and Lucas Cave are smaller than the other two study caves and show a greater fluctuation of

temperature. Tawney's Cave is the largest cave and shows a correspondingly smaller degree of temperature fluctuation.

Representative maximum-minimum temperatures during the summer months are shown in Fig. 5 for Lucas Cave. There was no fluctuation in temperature at Stations 2 and 3 in Tawney's Cave because of the continuous flow of air through the cave and past the stations. The maximum and minimum temperatures of Station 2 at any one date in Williams Cave and Lucas Cave differed by only a few degrees. There was no fluctuation in temperature during these months at Station 3 in any of the caves.

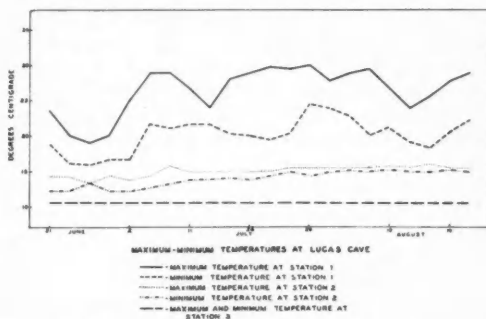


FIG. 5. Maximum-minimum temperatures at Lucas Cave during the summer, 1955.

Data obtained with the recording thermographs at Station 2 in each cave showed the same degree of fluctuation as that determined by maximum-minimum thermometers but demonstrated that a daily temperature lag also occurred. The lowest temperature occurred during the late morning hours (10:00-12:00 A.M.) and the highest temperature occurred during the evening hours (7:00-10:00 P.M.).

All temperatures recorded within the cave, except possibly the lowest temperatures recorded at Station 2 in some of the caves, are well within the range of tolerance of the salamanders, and temperature *per se* is hardly a limiting factor of the distribution of salamanders within the cave. There appeared to be no selected temperature between the limits recorded. No salamanders were found at temperatures below 8°C , though lower temperatures were recorded for Station 2 at Link Cave and Lucas Cave. The highest temperature at which a cave salamander was taken was 19°C in a crevice outside the mouth of Williams Cave. Bogert (1952) stated that the temperature of the substrate where terrestrial salamanders are found rarely exceeds 20°C , while the majority occur at temperatures of 15°C to 18°C . These latter figures do not hold, of course, for salamanders occurring in caves, since temperatures rarely reach these higher values in most of the twilight zone.

Although the temperatures fluctuate widely in part of the twilight zone, it is significant that the temperatures for Station 3 in all the caves remained rather constant at all seasons of the year. By moving rather short distances within the twilight zone ani-

mals may thus avoid any large fluctuations in temperature.

Air Movement

In single entrance caves air movement is the result of changes in temperature and barometric pressure. When the barometric pressure drops on the outside, air flows out, while the reverse occurs with increasing barometric pressure. When the temperature of outside air falls below the temperature of the cave air, a flow of air into the cave may result. An outflow of air is produced when temperatures within the cave reach a point above that of the outside air. These movements of air are usually of very small degree and hard to detect. Such limited movements of air are of little, if any, importance in the ecology of cave-dwelling animals.

Caves with two or more entrances may have an airflow through them of several hundred feet per minute. If the entrances are on the same level, wind may blow directly through the cave, but irregular and tortuous passages usually cause a great decrease in velocity. When one entrance is located above the other entrance(s), a cold air drainage may occur. The cold denser air moving out the lower entrance causes air to be pulled into the upper entrance. Once in the cave, this air is cooled and flows down and out the lower entrance. In the winter the opposite may occur, with air flowing out the upper entrance. Tawney's Cave falls into this category, but air was observed to flow out the lower entrance at all seasons of the year at a fairly constant rate, averaging 230 ft/min, with a range of 144-317 ft/min. This cool, moisture-laden air flowing from the lower entrance enabled the cave salamanders to occupy crevices as far as 15 ft outside the cave entrance proper, where, normally, adverse temperature and moisture conditions would prevent their occupancy. Temperature and saturation deficit at these areas were only slightly higher than within the cave. No air flow was detected with the anemometer at the other three study caves, and no salamanders were found outside the cave mouths.

An explanation of the continuous outflow of air at all seasons at Tawney's Cave remains to be made. Air flow in other caves has also been observed to occur in an inexplicable manner (Cournoyer 1954).

Precipitation

The distribution of precipitation over the period of study is shown in Figure 6. The average monthly rainfall for Giles County is given for the past 25 years. These data were obtained from weather records taken at Glen Lyn. The total monthly precipitation for the study period is also given for comparison. The monthly total rainfall from July to February during the period of study was below the average rainfall of these months for the past 25 years. This extended dry period resulted in the drying of the twilight zone mentioned above. In "normal" years, where the rainfall is evenly distributed throughout the year, a migration of salamanders into the deeper por-

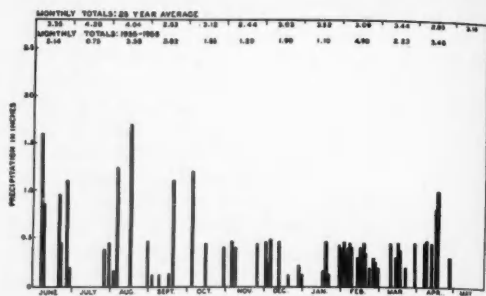


FIG. 6. Precipitation in Giles County, Virginia, during the period of study.

tion of the twilight zone may not occur. The salamanders began to reappear in the portion of the twilight zone nearer the mouths of the caves in February, and in April the animals were as close to the mouths as they had been during the preceding June. This was probably due, in part, to the increased rainfall in February and the resulting increase of water in the cave. The majority of salamanders seen in February and March were located on areas of the wall and floor where a thin film of water was flowing. During the preceding few months these same areas had been dry, and no salamanders were seen on them. Thus moisture in the cave and the saturation deficit were direct results of the amount of rainfall received by the surface areas above the cave.

Saturation Deficit and Moisture

Moisture appears to have a major influence on the distribution of salamanders within the cave. Only rarely was a salamander found in a crevice or on a wall that was not covered by a thin film of water. The greatest numbers were found in locations where water was slowly dripping down the wall or along a crevice.

The saturation deficit for each station is shown in Figure 7 for two of the caves and is representative of the other caves. The saturation deficit at Station 1 varied over a very wide range, as expected, while the range was much more narrow at Station 2 and the most narrow at Station 3. The least deficit was recorded at Tawney's Cave, where the air gained water vapor as it passed through the cave. A lag corresponding to that found in temperature is also seen in the saturation deficit data. The greatest fluctuation and earliest rise in saturation deficit occurred at Link Cave. The salamander population disappeared at about the same time (early August) that the saturation deficit increased. A comparison of these graphs with those showing population changes reveals a general correlation of lower numbers of salamanders with higher saturation deficits.

The moisture on the walls and in the floors of the mouths of the caves began to decrease in August, and this drying gradually extended into the twilight zones during the fall and winter months. In February and March the moisture began to increase and continued

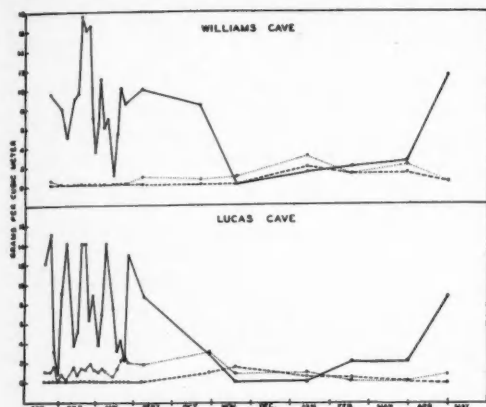


FIG. 7. Saturation deficit at Williams Cave and Lucas Cave during the year of study. The solid line represents Station 1; the dotted line, Station 2; the dashed line, Station 3.

to do so until April, at which time there appeared to be as much water in the form of a surface film on the walls as there had been during the preceding early summer months. As this drying out extended into the cave, the salamanders retreated deeper into the twilight zone. The average distance salamanders were found from the cave mouth increased during the late summer, fall, and early winter months and decreased during the spring and early summer. This is shown for Williams Cave in Table 1, with saturation deficit in grams per cubic meter also shown. The nature of the substrate prevented any type of moisture percentage determinations, and only saturation deficit is given in the table. A correlation does exist, however, between average distance from the mouth at which salamanders were taken and average saturation deficit. Saturation deficit affected the distribution of salamanders only indirectly by influencing the amount of moisture present on the walls and floor of the cave.

TABLE 1. Average distance of salamanders from the mouth of Williams Cave compared with saturation deficit.

Month	Number of Animals Captured	Average Distance From Mouth in Feet	Average Saturation Deficit at Station 2 cc/m ³
June	13	17.4	0.0
July	16	15.3	0.0
August	3	34.0	0.0
September	2	33.5	0.8
October	6	57.8	0.6
November	1	54.0	0.8
January	0	...	2.9
February	4	83.0	1.1
March	3	87.3	2.1
April	8	50.0	0.3

Evaporation

Black and white atmometer bulbs were used at each station in order to determine the relative amounts

of radiation (light) reaching each station, as well as differences in evaporation at each cave. Data obtained for this physical factor are given in Table 2. No evaporation occurred at Station 3 in any of the caves during the period of observation; therefore, no data are given for this station in Table 2. Evaporation differences between Station 1 at the caves are due to differences in overhead vegetation, exposure to wind, etc. Evaporation differences at Station 2, however, are due to differences of moisture conditions in the twilight zone and to the amount of light reaching the instruments. The difference in average evaporation per day between the black and white bulbs at Station 2 is 0.005 cc for Link Cave, 0.073 cc for Williams Cave, 0.085 cc for Lucas Cave, and none for Tawney's Cave. The small deflected entrance and the flow of saturated air past Station 2 in Tawney's Cave explain the absence of evaporation. The greatest difference occurred at Lucas Cave; thus, more light reached Station 2 in this cave than in the other study caves. The least difference occurred at Link Cave, where Station 2 was located behind a large pile of rock breakdown, consequently receiving very little light from the entrance.

Light

The amount of light reaching Station 2 and the length of the twilight zone are both dependent on the size of the cave entrance and the contour of the cave. The length of the twilight zone varies widely in the four study caves, being approximately 110 ft in Williams (total length of the cave), 100 ft. in Lucas, 70 ft in Link, and 150 ft in Tawney's.

The average light values obtained over the entire study period at Stations 1 and 2 are given in Table 3. The comparative amounts of light reaching Station 2 in each cave are similar to values obtained with white and black atmometer bulbs. Lucas Cave received the most light at Station 2, while Williams, Tawney's and Link Caves received less light in descending order. Differences at Station 1 are due to the direction of exposure of the cave entrance and to the amount of overhead vegetation at the cave entrance.

POPULATION STRUCTURE AND POPULATION DYNAMICS

Methods

During each visit to a study cave all accessible places were searched for salamanders, and data were recorded about each salamander captured. These data were sex, snout-vent length, total length, location within the cave, total distance from the cave mouth, and the temperature of the place at which the animal was taken. A system of toe-clipping similar to that employed by Blair (1941) was used to mark each individual captured. Sex was determined by the presence or absence of certain secondary sex characteristics, the males having a mental gland, papillose vent, and swollen region near the naso-labial grooves. Animals which were 125 mm or less in total length were listed as "juveniles." Sex of animals less than 125 mm in length, where given, was determined by exami-

TABLE 2. Evaporation in cubic centimeters at each study cave during the periods shown for each station.

Cave	Period	Station No. 1		Station No. 2		Station No. 1 Avg. Per Day		Station No. 2 Avg. Per Day	
		Black	White	Black	White	Black	White	Black	White
Link.....	53 days 24 June-16 Aug.	467.4	402.0	1.5	1.2	8.8	7.6	0.028	0.023
Williams.....	53 days 24 June-16 Aug.	409.6	387.1	16.6	12.6	7.7	7.3	0.311	0.238
Lucas.....	57 days 20 June-16 Aug.	794.3	700.3	131.3	126.4	13.9	12.3	2.303	2.218
Tawney's....	60 days 17 June-16 Aug.	645.2	567.1	0.0	0.0	10.8	9.5	0.00	0.00

TABLE 3. Average light in foot candles at the four study caves.

Cave	Station 1	Station 2
Link.....	750	0.5
Williams.....	820	2.0
Lucas.....	910	3.8
Tawney's.....	500	1.5

nation of the gonads and represent individuals taken from areas other than the study caves. Measurements were made by stretching the salamanders along a clear plastic rule. Snout-vent lengths were made by measuring the distance from the tip of the snout to the anterior edge of the vent. Measurements taken on live salamanders and on the same animals after preservation showed an accuracy in field measurements of ± 1 mm. Locations within the cave were designated by letters and numerals or by a short word description. Distances from the cave entrance were measured with a steel tape. All salamanders seen and positively identified, but not captured, were counted and the total number seen on each visit recorded. The "control caves" were visited at intervals throughout the study and the visible population of cave salamanders counted.

Changes in the Visible Population

The population changes in each study cave are plotted in Figures 8 and 9. An abrupt drop in the population of the study caves occurred at the very beginning of the year, but in the control caves the populations remained approximately constant during this period. This indicates that the salamanders are easily disturbed and that handling and toe-clipping result in their disappearance from the less concealed locations. This factor complicated the population studies during the more intensive summer study period but had little influence on the appearance of salamanders during the monthly visits, as indicated by visits at the same time to the control caves.

The initial population count was 20 at Link Cave, 15 at Lucas Cave, 13 at Williams Cave, and 3 at Tawney's Cave. From these initial counts the populations quickly dropped during the first part of July and remained rather low during the latter part of July and August. The visible populations remained at

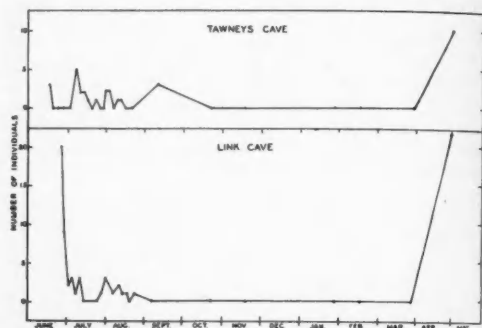


FIG. 8. Changes in the visible population at Tawney's Cave and Link Cave.

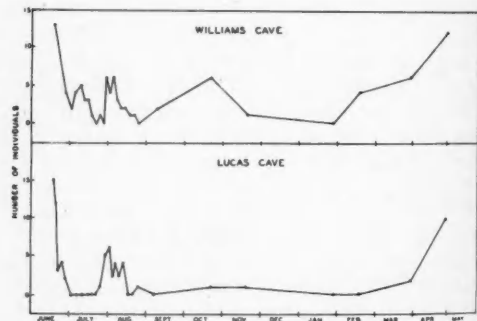


FIG. 9. Changes in the visible population at Williams Cave and Lucas Cave.

zero in Tawney's and Link Caves from October and September, respectively, to April, when the populations again increased to numbers comparable to the initial counts. At least one salamander was seen in one of the four study caves each month, except January, when no salamanders were seen.

A general pattern was noted in all of the caves. Populations reached a peak during the period of April to June, declined during July and August, and remained low during the fall and winter months. Such seasonal variation has also been observed in other species of salamanders. Fowler (1951) reported that *Plethodon dixi*, a cave-inhabiting salamander, shows a seasonal fluctuation in the visible population, with a peak during the summer months and a decline to a

low point during the winter. He points out that emigration from the cave is unlikely. Mohr (1944) described a migration of *longicauda* in a mine in Pennsylvania. Large numbers of the long-tailed salamanders entered the mine in March and April, emigrated from the cave in May, and returned in August and September. A seasonal fluctuation in the population of *Plethodon cinereus dorsalis* at Mammoth Onyx Cave in Kentucky has also been noted (Mohr 1952).

The disappearance of *lucifuga* in the study caves probably was not an emigration. As seen in Table 1, the average distance from the cave mouth increased as the population declined and decreased as the population began to increase. The few salamanders seen during the winter months were all in deep crevices in the inner part of the twilight zone, indicating that this species retreats into deep crevices. This movement may be partly due to a drying out of the cave, as pointed out above. The retreat into deeper crevices could occur as a result of slightly lower temperatures and a consequent hibernation of the animals, but this hypothesis appears unlikely since the salamanders seen during the winter were highly active, and temperatures in the darker end of the twilight zone were not extremely low, the lowest temperature recorded being 6°C.

A preliminary visit to Tawney's Cave on April 1, 1955, revealed a population of 23 salamanders, mostly adults. As seen from the graph, the visible population at this cave reached a maximum of only 10 animals during the study period, and these 10 were all immature. Only 8 of the total salamanders seen during the year were adults. The large percentage of juveniles seen during the study period indicates an increasing population. Apparently something had destroyed or displaced a large part of the population seen in April, 1955. An examination of the cave entrance and a query to the cave owner revealed the answer. On April 30, 1955, a group of local persons enlarged the cave entrance by tearing away rock which had served as hiding places for most of the salamanders seen on the preliminary visit. Large amounts of carbide were dumped in the entrance and about the cave mouth. The enlargement of the entrance was in preparation for a picnic in the cave the same night. A large number of persons entered the cave, and fires were built during the picnic. These changes of the cave environment undoubtedly caused the low number of salamanders and the higher percentage of juveniles observed during the following year.

Seasonal changes in the populations may not be as marked during these years in which the precipitation in the area is more nearly "normal" and more evenly distributed throughout the year. It can be seen from Figure 7 that the average monthly totals of precipitation in Giles County over a 25-year period are similar, while values obtained during the study period are usually well below the 25-year average. If the amount of moisture in the twilight zone governs the distribution of salamanders within the cave, as postulated

above, a study of populations over several years should reveal changes in the degree to which populations fluctuate.

Ives (1951) found the largest numbers of *lucifuga* to occur in February in an Eastern Tennessee cave, while none was present in April, June, November, and December. Since actual numbers are not given, it is difficult to compare the results of this study with those of Ives.

Recapture Data and Estimate of Populations

A total of 141 cave salamanders were captured in the study caves during the year of investigation. Of this total, 31 individuals were recaptured, giving an overall percentage of recaptures of 26.7%. The number of individuals marked and recaptured is given in Table 4.

TABLE 4. Marking and recapture data in the four study caves.

Cave	Total No. Captured	Number Marked up to Last Visit	Total No. Recaptured	Per Cent Recaptured
Tawney's.....	19	12	2	16.7
Link.....	35	27	5	18.5
Williams.....	47	41	12	29.3
Lucas.....	40	36	12	33.3

The Lincoln Index method of estimating population size was used. This is a proportional method that utilizes the following formula:

$$\frac{\text{No. of individuals marked in precensus period}}{\text{Other individuals in precensus period (x)}} = \frac{\text{Marked individuals captured in census period}}{\text{Other individuals captured in census period}}$$

$$x + \text{No. marked in precensus period} = \text{total population}$$

Allee *et al.* (1949, p. 269) point out two major sources of error in this method: (1) animals incapacitated in any way may redistribute themselves in a manner not like that of unmarked animals, and (2) emigration, immigration, and deaths are not accounted for in the formula. The small populations and small number of recaptures taken on any one visit do not permit the use of more elaborate statistical methods; thus, the Lincoln Index as used here may give only a rough estimate at best.

The period from June to July was designated as the precensus period and from July to April as the census period. Results obtained give the following population estimates:

Lucas Cave	62
Williams Cave	60
Link Cave	63
Tawney's Cave	36

These figures do not appear unreasonable from observations made during the study, and the author believes them to be a rather close estimate. The value obtained at Tawney's Cave is probably inaccurate, how-

ever, since only two marked individuals were recaptured and since the population was composed of large numbers of juveniles which may have migrated into the cave during the study.

Sex Ratios

Monthly changes in the sex ratios for the study caves are shown in Table 5. Immature individuals are not included. The total number of males in the caves was 86 and females 55, giving a sex ratio of males to females of 1.51. This departure from the expected ratio of 1:1 is significant as determined by the chi-square method. This numerical superiority of males was also found in each cave, except in Link (Table 6). Evidently, differences in sex ratios vary in different cave populations, ranging from 0.65 in Link Cave to 3.00 in Tawney's Cave. There is no apparent reason for the larger number of males.

TABLE 5. Monthly changes in sex ratio totaled for all study caves.

Month	Total No. Males	Total No. Females	Ratio Males/Females
June.....	35	21	1.67
July.....	11	13	0.85
August.....	9	7	1.29
September.....	4	1	4.00
October.....	4	1	4.00
November.....	1	0
January.....	0	0
February.....	3	1	3.00
March.....	3	0
April.....	15	11	1.36
Total.....	86	55	1.51

TABLE 6. Sex ratio at each study cave.

Cave	Males	Females	Ratio Males/Females
Tawney's.....	6	2	3.00
Link.....	15	23	0.65
Williams.....	33	21	1.60
Lucas.....	31	28	1.10

Most of the gravid females were captured in late July and August, a time during which only 14.8% of the total number of salamanders was captured, and selective collecting due to habits during the egg-laying period could hardly result in the total departure observed.

There was no evidence from the recorded distances moved that male salamanders were more active than female salamanders or that females were more active than males. No difference in selection of the more concealed crevices by either sex was noted. The observed sex ratios may actually approximate the true ratios, except in Tawney's Cave, where the small sample precludes any attempts to arrive at an accurate ratio.

Juveniles composed 11.35% of the 141 animals

marked. Ten of the 16 juveniles were captured in Tawney's Cave, 5 in Williams Cave, and 1 in Lucas Cave. None was taken in Link Cave. They were distributed over the year as follows.

June	1
July	6
August	1
October	1
April	7

The groups of young taken in July and April both averaged 42 mm in snout-vent length and approximately 110 mm in total length. Recaptures of young marked animals were not sufficient to determine rate of growth, but it is likely that these two groups represent animals of the same age, indicating a prolonged breeding season, or possibly, more than one breeding season each year.

NATURAL ENEMIES

Little is known concerning the kinds of predators that feed upon the cave salamander and its ecological relationships with them. Banta (1907, Fig. 13) indicated that the mouse *Peromyscus* was probably the chief predator on the cave salamander at Mayfield's Cave, but no data are given to support this indication. The author has been able to find no other references to predation on *Lucifuga*. Nevertheless, many animals probably utilize it as prey. Probable mammalian predators in the study area include the raccoon (*Procyon lotor*), weasel (*Mustela frenata*), mink (*Mustela vison*), spotted skunk (*Spilogale putorius*), striped skunk (*Mephitis mephitis*), red fox (*Vulpes fulva*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), various field mice (*Peromyscus*), mole (*Scalopus aquaticus*), shrews (*Sorex*), and the opossum (*Didelphis virginiana*). The most abundant mammal in the study caves is the cave rat (*Neotoma magister*), but the probability of this rodent feeding on salamanders is unlikely. Examination of the stomach contents of seven cave rats trapped in the study caves revealed only vegetable matter. Of the animals listed above, the presence of skunks, foxes, raccoons, and possums in the study caves was revealed by tracks, scats, and sight records. These animals probably represent the more frequent mammalian visitors which may be regarded as predators to the study caves. Snakes, especially the garter snake (*Thamnophis sirtalis*), ring-neck snake (*Diadophis punctatus*), milk snake (*Lampropeltis dolia*), and pilot blacksnake (*Elaphe obsoleta*) may comprise the chief enemies of cave salamanders. All of these snakes have been seen or collected at the mouth or in the twilight zone of the caves in the study area. The probability that most of these snakes take salamanders as food is supported by the studies of Uhler, Cottam & Clarke (1939) on the food of snakes in the George Washington National Forest, Virginia.

No attempt was made in this study to identify endoparasites, but their presence was noted when specimens were dissected for study of food items or gonad condition. Almost all stomachs examined contained

catenoid colonies of the protozoa *Haptophyra* sp. Nematodes were also usually present in the stomach or intestine, as well as in other organs. The ectoparasitic chiggers (*Trombicula*), often reported from reptiles and amphibians, were not seen on the salamanders studied.

FOOD

Noble (1931, p. 417) pointed out that no species of urodele is known to limit its diet to a specific kind of animal food. Hairston (1947) stated that "the differences between the species are to be viewed as effects rather than causes of differing habitats, since salamanders will eat almost any animal that falls within the proper size range." Farner (1947) reported that two salamanders, although feeding in the same habitat, did not eat the same food; at Crater Lake, Oregon, *Ambystoma macrodactylum* was apparently a scavenger, whereas *Taricha granulosa mazamae* was primarily predaceous. Smith (1948) studied the potential food and food habits of several cave-dwelling amphibians in Missouri and found no predilection in food habits; *E. lucifuga* and *Typhlotriton spelaeus* occupied the same habitat and consumed the same kind of food.

E. lucifuga and *E. longicauda* are found in caves in Virginia, and the possibility of competition for food, or difference in food habits, led to a study of their food habits. Ten *longicauda* and 13 *lucifuga* were preserved immediately after capture and the stomachs and intestines later removed and analyzed. The food items found were identified only to order, and, in a few instances, to family. Table 7 gives the percentage of occurrence of the food items identified in the two species. Dipterans composed the largest percentage of food items identified in both species, and the majority of these flies were the helomyzid, *Amoebalaria defessa*, probably the most abundant food item in the caves from which the salamanders were taken. These flies were numerous in all parts of the caves, even within a few feet of the entrance. The other predominant food items of *lucifuga* were mites and ticks (53.8%), lepidopterans (46.2%), and pseudoscorpions (38.5%). The other major food items of *longicauda* were isopods (40.0%), orthopterans (30.0%), and coleopterans (30.0%). In general, the food items found occurred in both species, and there is no apparent predilection of either species to a particular type of food.

Tipulids, coleoptera, diptera, a minute gastropod, and rock and plant material have been reported from the stomachs of *lucifuga* in Maury County, Tennessee (Barr 1949).

Both *lucifuga* and *longicauda* probably feed by shooting out their tongues to catch prey. Brandt (1946) reports that *lucifuga* feed on small soft-bodied roaches by shooting out their tongues to about one inch. Blanchard (1925) kept *lucifuga* alive as long as 14 months in the laboratory on a diet of fruit flies and earthworms. The author has observed the feeding process in both these species. Both fed on *Drosophila*

TABLE 7. Percentage of occurrence of the food items in the stomachs and intestines of 13 *Eurycea lucifuga* and 10 *E. longicauda*.

Food	<i>E. lucifuga</i> (13)		<i>E. longicauda</i> (10)	
	No. of stomachs in which food occurred	Percentage of occurrence	No. of stomachs in which food occurred	Percentage of occurrence
Diptera—total.....	9	69.2	7	70.0
Drosophilids.....	3	23.1	2	20.0
Holomyzids.....	9	69.2	8	80.0
Sarcophagids.....	5	38.5	0
Tipulids.....	2	15.4	1(?)	10.0
Orthoptera.....	2	15.4	3	30.0
Coleoptera.....	2	15.4	3	30.0
Thysanoptera.....	2	15.4	0
Lepidoptera (scales).....	6	46.2	1	10.0
Collembola.....	4	30.8	1	10.0
Hymenoptera (ants).....	3	23.1	1	10.0
Insect larvae (unidentified).....	2	15.4	1	10.0
Phalangids.....	2	15.4	1	10.0
Diplopoda (Pseudotremia).....	0	1	10.0
Chelonethida (Pseudoscorpions).....	5	38.5	2	20.0
Aranidae.....	0	1	10.0
Acarina—total.....	7	53.8	1	10.0
Mites.....	4	30.8	1	10.0
Ticks.....	5	38.5	0
Isopoda.....	3	23.1	4	40.0
Cast skins.....	4	30.8	2	20.0
Plant remains.....	2	15.4	0
Sand Grains.....	13	100.0	10	100.0

placed in aquaria while in captivity and remained in good condition over a period of six months.

COMPETITION

Crombie (1947), who thoroughly reviewed the subject of competition between species, and Hairston (1951), who concluded that interspecific competition is responsible for abrupt vertical limits of distribution of *Plethodon glutinosus* and *P. jordani* in the Southern Appalachians, point out the complexity and difficulty in analysis of interspecies competition. Hairston lists three criteria which have been used to demonstrate interspecific competition in nature: "(1) closely related species are in competition when they occur together, (2) species having one or more ecological requirements in common are in competition, (3) species having mutually exclusive ranges or stations at their zones of contact are in competition at their zones of contact."

Observations in the field led the author to believe that interspecific competition may occur between *lucifuga* and *longicauda*, at least in the area of study in Virginia. The two species were often found together in the twilight zone of caves and in other moist areas containing limestone rocks. *E. lucifuga* appeared to be more prevalent in caves when both species were present, but in Montgomery, Pulaski, Roanoke, and Bath Counties, Virginia, where no *lucifuga* have been seen or reported, *longicauda* was apparently present in comparatively larger numbers than in areas where the two species occur together.

In order to show the difference in occurrence of the

two species, a "frequency of co-occurrence graph" was devised (Fig. 10). The number of individuals of one species is placed on the ordinate, while the number of individuals of the other is placed on the abscissa. The numbers of samples (cave visits) are represented by black circles, the size of the circle being proportional to the number of samples. For example, it can be seen from Figure 10 that there were 8 samples in which 4 *lucifuga* and 0 *longicauda* were found, 3 samples in which 1 individual of each species was found, etc. If these two species occurred together in randomly distributed numbers, a situation which would probably indicate a lack of competition or ecological segregation, the number of samples represented by black dots should fall in a random manner, with the average occurring on a diagonal representing approximately equal numbers of each species. From Figure 10, it is readily seen that just the opposite occurs with these two species, the greater concentrations of samples containing predominantly one or the other species. This demonstrates some type of segregation between the two. This segregation could be due to differences in ecological requirements, such as feeding habits, moisture, substrate, etc., or to interspecific competition. Since both species have similar feeding habits and since both are frequently found in caves with similar ecological conditions throughout their ranges, it appears that the second explanation—that of competition—may be the correct one. Although these data are far from conclusive, they do suggest that *lucifuga* and *longicauda* compete with one another.

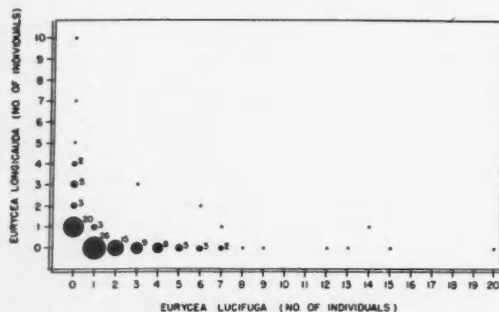


FIG. 10. The frequency of co-occurrence of *Eurycea lucifuga* and *Eurycea longicauda* in 114 samples of caves in Virginia. For full explanation see text.

This competition could be for food, suitable crevices and hiding places in the twilight zone, or a combination of a number of factors. The feeding habits of these species are similar, as pointed out above, and suitable moist crevices are few in many twilight zones. These data are at least consistent with an explanation of competition. A complete detailed analysis of all possible explanations must be made before competition between two species of *Eurycea* is proven.

Mohr (1944) reports that no *longicauda* were seen in more than 100 visits to Pennsylvania caves, though this species frequents mines and springs in the area. *E. lucifuga* apparently does not occur in Pennsylvania.

In the western part of its range, *longicauda* has often been reported from caves. It appears that this species does not always frequent caves when they are available, even in the absence of *lucifuga*. This fact further complicates any attempt at an analysis of competition between these species.

LABORATORY STUDIES

DEHYDRATION

All animals used in the laboratory studies were obtained from caves in Giles and Montgomery Counties, Virginia, with the exception of *Aneides aeneus*, which came from caves in the vicinity of Natural Tunnel, Scott County, Virginia. These caves had approximately equal temperatures and humidities at the time of collecting.

Several investigators have shown that the ability of amphibians to survive water loss is correlated with ecological habitat (Thorson & Svihla 1943, Littleford, Keller & Phillips 1947, Gordon 1952, Thorson 1955, Cohen 1952). Observations made during the field studies suggested that *lucifuga* and *longicauda* were generally found in places of different water availability. *E. longicauda* was most often taken from along wet stream banks on wet rocks, beneath moist logs, and in the wetter portions of the twilight zone of caves. Several adults were taken at night from water, where they were swimming. Hurter (1911) reports this species from similar situations. Several other authors report their occurrence beneath stones along streams (Minton & Minton 1948, Smith 1950, Reynolds & Black 1936, Bishop 1943, Morse 1901, Ditmars 1905, Bishop 1941, Holbrook 1842). *E. lucifuga* is also semi-aquatic but appears to be more terrestrial than *longicauda*. Only one adult was seen swimming in water during the course of this study, and many individuals seen in caves near the entrance were in relatively dry crevices. They do, however, show a preference for rocks which have a thin film of water on them.

In order to compare this apparent difference of the two species, a dehydration apparatus similar to that used by Hall (1922) and Thorson & Svihla (1943) was utilized. Air was drawn through the apparatus by means of a Cenco vacuum pump, passing first through a Sargent wet test flow meter, which provided an even and measured flow of air of 3000 ml per minute. The air was then bubbled through three bottles of sulfuric acid to remove all moisture and then passed through a bottle of sodium hydroxide to neutralize any acid. Pieces of litmus were used to check the neutrality of the air. A short column of calcium chloride was placed in the system and occasionally weighed to insure that no weight gain from water had occurred. The dried air was then led into a three-necked distillation flask equipped with a wire screen floor to allow free circulation of air on all sides of the animal. A thermometer was placed in the dehydration chamber at the level of the wire floor, and a water bath surrounding the chamber maintained the temperature at 20°C, plus or minus one degree. Prior

TABLE 8. Data on vital limits of water loss in *Eurycea lucifuga* and *E. longicauda*.

Number and Sex	Original Wgt.	Final Wgt.	Wgt. Loss	Per Cent Body Wgt. Lost	Survived	Duration Run Mins.	Per Cent Body Average Wgt. Lost
<i>Eurycea lucifuga</i>							
1. F.....	3.492	2.535	0.957	27.4	Yes	82	
2. F.....	3.792	2.812	0.980	25.8	No	69	
3. M.....	3.180	2.030	1.150	36.2	Yes	43	
4. M.....	2.887	2.176	0.711	24.6	No	61	
5. I.....	0.733	0.527	0.206	28.1	No	26	
6. M.....	2.784	2.108	0.676	24.3	No	34	27.7
<i>Eurycea longicauda</i>							
1. F.....	4.015	3.502	0.513	12.8	No	50	
2. I.....	2.085	1.896	0.189	9.1	Yes	30	
3. M.....	2.621	2.324	0.297	11.3	No	23	
4. M.....	2.459	2.216	0.243	9.9	No	27	
5. F.....	3.871	3.560	0.311	8.0	Yes	21	
6. F.....	4.233	3.375	0.498	11.8	No	65	
7. F.....	3.952	3.588	0.364	9.2	Yes	21	
8. F.....	2.948	2.363	0.585	19.8	Yes	69	
9. M.....	2.467	2.068	0.399	16.2	No	26	
10. F.....	2.782	2.542	0.240	8.6	Yes	..	11.7

I=Immature F=Female M=Male

to this experiment all test animals were acclimated at 18°C and 100% relative humidity for 7-10 days. Test animals were washed to remove any extraneous material, blotted on absorbent paper to remove excess water, weighed, and placed in the desiccation chamber until cessation of throat movements, whereupon they were removed and immediately weighed.

Results are shown in Table 8 where it is readily seen that *lucifuga* has a higher (27.7) percentage of water loss at the vital limit than does *longicauda* (11.7). The range of water loss in *lucifuga* was 24.3-36.2% of the total body weight, while that of *longicauda* was 8.0-19.8%. No burrowing or digging response of these two species occurred during the experiments. Gordon (1952) reports such a response in *Plethodon jordani melaventris* and none in *Aneides aeneus*. Both *lucifuga* and *longicauda* attempted to escape by climbing up the walls of the desiccation chamber during the later stages of dehydration.

Littleford, Keller, & Phillips (1947), using an air flow of 1000 ml per min, report an average per cent water loss of 18.04 in eight *E. bislineata bislineata*, a relatively more aquatic species. Differences in experimental procedure make it difficult to compare results obtained by previous investigators, except in a general way. From a knowledge of habitats one would expect that *E. b. bislineata*, would have a lower vital per cent of water loss than either *lucifuga* or *longicauda*. Gordon (1952) reports a water loss of 30.4% in *Aneides aeneus*, probably the most terrestrial genus of plethodontid salamanders (Storer 1925).

The comparison of *lucifuga* and *longicauda* shows a correlation of habitats with ability to survive the loss of body water.

CRITICAL THERMAL MAXIMA

Cowles & Bogert (1944) defined the critical thermal maximum (CTM) as the point at which locomotor activity becomes disorganized and the animal is incapable of escaping from continued conditions that will lead to its death. Lowe & Vance (1955) modified this concept for a population to include the range of variation, with the CTM as the arithmetic mean of the collective thermal points.

Little investigation of upper thermal limits has been made in amphibians. Stebbins (1945) gave data on *Ensatina eschscholtzi*; McFarland (1955) studied lethal limits in *Taricha torosa*; and Zweifel (1957) studied CTM and acclimation of the CTM in eleven species of plethodontid salamanders of Western Virginia and found interspecific differences of animals collected from the same area and acclimated at the same temperature.

E. lucifuga, *E. longicauda*, and *Aneides aeneus* were collected from caves in Western Virginia for use in this experiment, and it is likely that the past ecological histories of the individuals used are similar, since they were taken from caves with very similar ecological conditions. All animals used were acclimated at 18°C and 100% humidity for two weeks prior to their utilization in this experiment. An animal chamber made of a large three-necked distillation flask was immersed in a water bath equipped with a stirrer. Air was supplied to the flask by means of an aquarium pump and was warmed to the temperature of the water in a copper coil. The animal was placed on a brass-gauze floor to allow an even circulation of the warmed air on all sides. A thermometer was placed in the flask with the bulb at the level of the

gauze floor. Heat was supplied by two gas burners placed beneath the water bath, and temperatures were recorded to the nearest 0.1°C.

All salamanders exhibited a series of symptoms similar to those mentioned by Zweifel (1957) for aquatic species and exhibited the following characteristic behavior: as the temperature of the air was increased, the salamander increased its activity, rapidly climbing up the walls of the flask in attempts to escape. This action was followed by violent leaping movements and more frantic attempts to escape, loss of coordination of limb movement, extremely rapid throat pulsation, and finally, spasms characterized by twitching movements of the whole body, particularly the head and tail. This last mentioned symptom was taken as the end point (CTM) and was immediately followed by heat rigor. Temperature of the air flask was recorded at the onset of spasms.

Data obtained in this experiment are given in Table 9. There is no significant difference in the CTM of *Aneides aeneus*, *Lucifuga*, and *Longicauda*, and the range of variation overlaps in all three species.

TABLE 9. Data on Critical Thermal Maxima for three species of Salamander.

Species	Mean	Number	Range
<i>Eurycea lucifuga</i>	34.14	11	33.6-34.7
<i>Eurycea longicauda</i>	33.79	13	33.2-34.5
<i>Aneides aeneus</i>	34.33	9	34.2-35.5

Aneides aeneus, however, shows a slightly higher CTM than the *Eurycea*, and this again, as in dehydration, correlates with the greater terrestriality of this species.

Zweifel (1957) records CTM values for *E. b. bislineata* at 34° and 35°C, which is within the range of variation for the other two species of *Eurycea* mentioned above. Interspecific differences of CTM are not significant for these species.

ACTIVITY

Periodic activity in salamanders has been the object of few laboratory studies. Rhythmic activity independent of environmental factors has been demonstrated in few, if any, adult salamanders.

Both *lucifuga* and *longicauda* were tested for activity by means of an activity recorder (Aktograph) modified from that of Gunn & Kennedy (1936). It is essentially a box pivoted on a knife edge at its median transverse line. A counter-swung weight placed on a rod extending below the upper box serves to place the center of gravity below the whole. A vane on the lower end of the counterweight-rod serves as a damper as it moves back and forth in water. An arm from one end of the upper box serves as a writing arm on a kymograph. The upper box is fitted with a thermometer and air ports and a floor of brass gauze. Beneath this floor several baffles are used to prevent movement of humidity-controlling

solutions. Sensitivity of the apparatus is adjusted by manipulating the weights and the amount of water in the lower box. The apparatus when balanced is sensitive to 0.5 grams. Any movement of an animal along the longitudinal axis of the upper box tilts this box and inscribes on the kymograph.

Figure 11 shows sample results obtained at 18°C and 100% relative humidity. These typical records show, essentially, the same pattern found in 38 runs using *lucifuga* and 46 runs using *longicauda*. All but one *lucifuga* showed only random movements during the 24-hr test periods. The one exception was an activity period from 9 to 12 P.M., with no other movement during the 24-hr test periods. All but two *longicauda* showed activity periods of approximately two hours, all within a period from 2 P.M. to 9 P.M.; these two showed random activity comparable to that of *lucifuga*.

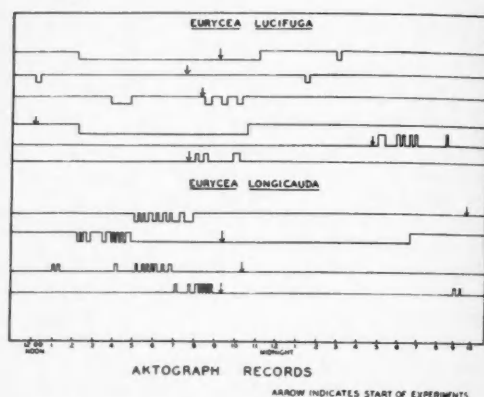


FIG. 11. Typical activity patterns of *Eurycea lucifuga* and *Eurycea longicauda* as shown by Aktograph recordings.

This activity pattern in *longicauda* appears to be of an endogenous type (Park 1941), but it is not known if it is habitual activity or inherent activity. Support for the latter classification is furnished by the fact that *longicauda* still exhibited this rhythmic pattern after being kept in captivity for four months in total darkness and at 18°C.

The activity pattern shown here experimentally is not supported by field observations of Mohr (1944) on a large population of *longicauda* in an abandoned mine in Pennsylvania. Mohr reports that visits to the mine at almost every hour of the day revealed no differences in activity, the salamanders often remaining motionless for hours at a time. The author, however, has taken *longicauda* outside of caves only during the early evening hours. In the twilight zone of caves, it is usually well concealed during daylight hours but has often been seen abroad during darkness. A detailed study of marked individuals during 24-hour periods in a large population is necessary before activity periods can be shown to occur in the field.

Observations made by the author on activity in the field every two hours for periods of 24 hours indi-

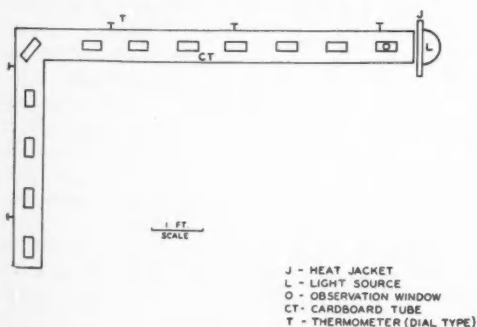
cate that *lucifuga* is arrhythmic. Sinclair (1950) states that in Tennessee caves this species is found abroad during the day, as well as at night, but in terrestrial situations away from caves it seeks shelter during the day and wanders out at night. Apparently, adverse conditions of temperature and humidity prevent diurnal activity in an epigeal habitat.

REACTIONS TO LIGHT

Investigations on the reaction of salamanders to light have shown that most of the species tested were negatively phototropic (Reese 1906, Pearse 1910, Cole, 1922, Bishop 1927, Vernberg 1955). In order to determine the reaction of *lucifuga* and *longicauda* to light, two experiments were devised, both using only white light supplied by a 25 W bulb.

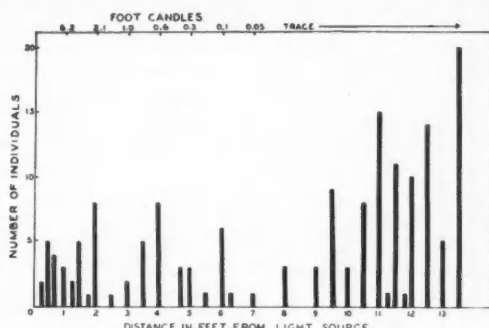
A light gradient apparatus (Figure 12) was constructed from round cardboard tubes six inches in diameter and 13.5 feet in length, with a right angle bend at 7.5 feet. The interior of the tube was water-proofed by coating with melted paraffin. Observation windows were cut along the top and provided an adequate view of the interior. Thermometers were placed at different intervals along the tube and were checked periodically to insure that no temperature gradient was present. A 6-in desk lamp reflector was behind the electric light bulb, and a heat jacket of four plates of glass with dead air space between the plates was in front of the light source. The entire apparatus was located in a room with a temperature of $17.5^{\circ} \pm 1^{\circ}\text{C}$ and in total darkness. One-half inch of water was kept in the bottom of the tube at all times to insure a high humidity. The greatest temperature gradient observed during the experiment was 1.0°C throughout the length of the tube. Various numbers of *lucifuga* were placed in the tube and their position checked periodically after they had been there at least two hours. Light readings were taken at different spacings with a Weston photometer.

Results for 23 observations are shown in Figure 13. Although these results show that *lucifuga* is negatively phototropic, many individuals were observed only inches from the light source, even after being in the



LIGHT GRADIENT APPARATUS

Fig. 12. Diagram of apparatus used in determining the reaction of *Eurycea lucifuga* to a light gradient.



DISTRIBUTION OF *EURYCEA LUCIFUGA* IN AN EXPERIMENTAL LIGHT GRADIENT AT 100% HUMIDITY AND $17.5^{\circ} \pm 1.0^{\circ}\text{C}$ GRAPH REPRESENTS A TOTAL OF 23 OBSERVATIONS.

FIG. 13. The distribution of the cave salamander in an artificial light gradient.

tube for as long as 48 hours. Apparently, this negative reaction to light was not a strong one, and a second and simpler experiment, similar to that of Vernberg (1955), was used to test this reaction further. A box was divided into two compartments by a partition. This partition had holes at the base which permitted the animals to pass freely from one compartment to the other. A light bulb was placed over one compartment, and the other compartment was covered with a lid. Salamanders were placed in the box singly, and observations were made at varying intervals to determine the compartment occupied by the animal. Both *lucifuga* and *longicauda* were used in this experiment. The results obtained are given in Table 10.

TABLE 10. Reactions of *Eurycea lucifuga* and *E. longicauda* to light.

	<i>E. lucifuga</i>		<i>E. longicauda</i>	
	Dark Side	Light Side	Dark Side	Light Side
Number.....	31	24	31	7
Per cent.....	56.4	43.6	81.6	18.4

Both of these experiments indicate that *lucifuga* is only slightly negative in its photic reaction. The second experiment shows that *longicauda* is much more photo-negative than *lucifuga*. A similar reaction of *lucifuga* to light was also observed in the field. The observations of Banta & McAtee (1906) that the larvae quickly retreated when a light beam was placed on them, while the adults were not disturbed by light, have been supported by the author. Only in a very few cases have individuals of this species retreated from a light beam in caves, and this reaction may have been due to a disturbance other than light. Individuals have been observed in the twilight zone of caves during the day, where they were often exposed to as much as 25 foot-candles of light near the mouth, again indicating their weak reaction to light.

DISCUSSION

The cave environment, with its stability of environmental conditions, is a naturally favorable habitat for many organisms. However, animals in a true cave environment may meet two difficulties: (1) the usual paucity of food and the ultimate dependence upon an epigeal food source, and (2) the complete absence of light. The crepuscular, or twilight, dwellers do not usually meet these difficulties, yet have the advantage of a relatively stable environment. Being closer to the primary producers, food is usually abundant in the cool and moist twilight zone, and perpetual darkness is lacking. Although the temperature and moisture conditions vary, this fluctuation is much less marked and is more gradual than in an epigeal habitat. Numerous animals whose habitats are normally outside caves are often found in cave twilight areas, where they undoubtedly find very suitable conditions. Many invertebrates and vertebrates have been reported from the crepuscular zone of caves (Fowler 1943, Fowler 1946, Barr 1949, and others) in the United States. These lists contain many species of amphibians which frequent caves, but only *E. lucifuga*, *Plethodon dixi*, and possibly *E. longicauda melanopleura* can be considered as having their primary habitat in the twilight zone of caves. It is indeed surprising that more species of amphibians have not adopted the cave twilight zone as a primary habitat. From all of the factors examined in this study, the cave salamander appears to be well adapted to this environment. The well-developed limbs and prehensile tail of this species are well adapted for climbing about the walls and crevices of caves. The eyes are large and well developed for a crepuscular existence (Eigenmann 1899). Almost any animal food which can be swallowed is utilized. The salamanders have often been observed feeding on dipteran larvae, which in turn were feeding on carcasses of larger animals which had fallen into the caves and died. The species is certainly not strongly, if at all, negative in its reaction to light and is to be found abroad during day as well as night. Like animals which live deep in caves and underground streams, *lucifuga* appears to be arrhythmic. This absence of a strong phototropism may have developed in the absence of strong selective pressures. The animal can undergo a greater water loss without deleterious effects when subjected to dehydrating conditions than can its closest relative, *longicauda*. This may be an important factor in prowling for food outside the mouth of caves or when the animal is not living within a twilight zone.

Dunn (1926) stated that "almost any small spring or stream in the animal's range is utilized. The cave habitat of *melanopleura* and of *lucifuga* (and of *longicauda* as well in those localities) is best explained by the fact that most of the small springs and brooks in their range are cave springs and cave brooks. Where there are springs and brooks outside of caves in their range the animals occur there as well as in caves." These statements are undoubtedly true for *melanopleura* and *longicauda*, but evidence

has been presented here indicating that *lucifuga*, almost without exception, is from limestone regions, and that the greatest majority of records are from caves. Springs and brooks occur on non-limestone areas within the range of *lucifuga*, but as far as the author knows the only record of the occurrence of *lucifuga* any distance from limestone (and possibly sandstone) areas is in Habersham County, Georgia. *Eurycea lucifuga* probably occurs in limestone caves more often than in epigeal habitats because the cave habitat, with its adequate cracks and crevices, adequate food, and favorable temperature and moisture, is better suited to the requirements of the species.

The entrance of salamanders into a cave habitat has been explained partly on the basis of negative phototropisms in the animals (Mittleman 1950). This is hardly a causal factor, especially in *lucifuga*, where experimental work indicates only a very slight and insignificant negative reaction to light.

The ecological factors which limit the distribution of the cave salamander are difficult to determine. The main factor appears to be the absence of limestone. This cannot be the only factor, since limestone areas extend well beyond the present range of the animal. For example, limestone belts in the Appalachian Valley are continuous, or nearly so, through Tennessee, Virginia, Eastern West Virginia, and into Pennsylvania, but no *lucifuga* have been reported from Pennsylvania in spite of searches by several collectors (Mohr 1953). Climatological factors probably account for this type distribution. Lower temperatures to the north, higher temperatures to the south, and low precipitation to the west may play important parts in limiting the range. Distribution to the east most likely is limited by the absence of limestone in eastern Virginia, North Carolina, and South Carolina.

The local distribution of *lucifuga* is even more difficult to analyze. The absence of this salamander from Montgomery, Roanoke, and Pulaski Counties, Virginia, is difficult to explain, since environmental conditions are apparently the same as those in caves only thirty miles away, or less, where *lucifuga* occurs. This absence may be due to competition with other species, notably *E. longicauda*, *Plethodon dixi*, and *P. wehrlei*. The last two species apparently do not occur with *lucifuga* in other parts of Virginia. *Aneides aeneus* and various species of *Plethodon* and *Eurycea* may compete with the cave salamander in other parts of the range. It is also likely that such local patterns of distribution are governed by ecological factors which were not measured or were overlooked.

The selection of a cave twilight zone habitat by *lucifuga* and by *longicauda* in certain areas may also be due, in part, to the effects of man in the clearing of land for agriculture and by lumbering in most areas of the ranges of these two species. The destruction of much of the original habitat may have forced the salamanders into a twilight zone habitat when caves were locally available. Gordon (1952)

suggests that *Aneides aeneus* may have been forced into a rock crevice habitat by similar factors.

Mittleman (1942) proposed that *Lucifuga* be considered a race of *longicauda*. This proposal was based upon four specimens from Tennessee and Kentucky which supposedly show intermediate characters. The very apparent differences between these species shown by laboratory experiments indicate a wide difference in their physiology. The differences in dehydration, activity, and reactions to light are greater than one would expect if races of the same species were compared. The possibility of competition between the two forms, their occasional co-occurrence, and the absence of other intermediates from more of their overlapping ranges (Neill 1954, Martof & Humphries 1955) also make Mittleman's proposed taxonomy of these two forms untenable (Hutchison 1956b). As far as the author is aware, Mittleman's allocation has been followed in only two subsequent papers (Mittleman 1950, Mohr 1950).

Lack, working with birds, showed that two congeneric birds living in the same habitat have distinctive feeding habits and he has also shown that this holds true for a large number of species of different genera (Lack 1944, 1945, 1946). Several authors have referred to Gause's hypothesis in their works. Lack (1945, 1946) states this hypothesis by writing, "Gause contends that two species with similar ecology cannot live in the same area." Williamson (1949) and Green (1951) state the so-called Gause's hypothesis by saying that "no two species in the same habitat have the same ecology." Gilbert, Reynoldson & Hobart (1952) point out that the terms used in the above statements are somewhat subjective and that the term "similar ecology" is "objectively meaningless." On the same grounds the phrase "objectively meaningless" is fully as objectionable as "similar ecology." The generalized statements of Lack, Williamson, and Green quoted above do not need more exact statements concerning the degree of similarities, the spatial limits of any competition or even to mention the relative sizes of populations to be of value as a hypothesis or principle. Any two species will vary widely in regard to these and most other ecological factors and each set of conditions must be analyzed with these factors in mind. Admittedly, any analysis of competition under field conditions is apt to be perilous and the extension of results of culture experiments, as performed by Gause on protozoa, flour beetles, and yeast, to populations in the field is conjectural. Although Gilbert, Reynoldson, & Hobart point out that Gause draws no conclusions from his experimental work and makes no statement which resembles the hypothesis bearing his name, the concept of the so-called Gause's hypothesis does not appear to be invalidated. The hypothesis may not have been stated by Gause, but the principle involved was first clearly demonstrated by him.

Evidence has been presented that indicate *Lucifuga* and *longicauda* eat the same types of food (Table 7). It has also been shown (Fig. 10) that these two species

do not usually occur together in the twilight zone of caves, but in the absence of *Lucifuga*, the long-tailed salamander may be comparatively common in such a habitat. This situation may certainly indicate competition between the two species, in which case, it appears that the conclusions drawn from Gause's experiments concerning competing organisms applies. When *Lucifuga* is occasionally found in an epigeal habitat it occurs in the same types of places that *longicauda* is usually expected. The cave salamander appears to be the more specialized of the two species (Dunn 1926). The adaptation of *Lucifuga* to a twilight zone existence probably has resulted in mechanisms which reduce competition between it and *longicauda*, the more epigeal of the two.

SUMMARY

1. This study of *Eurycea lucifuga* consisted of three parts: (1) distribution and habitat selection, (2) field studies on population structure, population dynamics, environmental factors, food, habitats, and competition, (3) experimental laboratory work on activity, critical thermal maxima, reactions to light, and vital limits of water loss of *E. lucifuga* and *E. longicauda longicauda*.

2. The known range of *Lucifuga*, based on museum specimens and literature records, is from Tippecanoe County, Indiana, in the north, to Polk County, Georgia, in the south, to Mayes County, Oklahoma, in the west, and Rockbridge County, Virginia, in the east.

3. With the exception of only one locality record, all *Lucifuga* have been taken in limestone areas. Experiments indicate that this correlation of distribution with limestone is not due to the limestone, *per se*, but probably to the habitat of caves afforded by the soluble rock.

4. Four study caves and three control caves were selected for study in Giles County, Virginia, in the Appalachian Valley and Ridge Province. Visits to the study caves were made every three days from June through August, 1955, and once each month from September, 1955, to April, 1956, except for December.

5. Recorded temperatures never dropped below 6°C or rose over 15.5°C in the twilight zones of the study caves. The twilight zones showed only a few degrees fluctuation throughout the year. A temperature lag of a month or more was recorded in the twilight zones and deeper parts of the cave after outside temperature trends changed. A daily temperature lag was also observed. The temperatures recorded in the caves appeared to be well within the range of tolerance of the cave salamanders.

6. The most important factor governing the distribution of salamanders within the twilight zone appeared to be moisture, the higher the saturation deficit in the twilight zone, the deeper the animals were found in the cave. The amount of moisture in the twilight zone is a direct result of precipitation, and the visible population changes appear to be governed to a great degree by moisture conditions.

7. The length of the twilight zone is a result of the size of the cave entrance and contour of the cave. The length of the twilight zone varied from 70 ft in Link Cave to approximately 150 ft in Tawney's Cave.

8. Air movement was detected in only one study cave. In Tawney's Cave air flow through the cave averaged 230 ft/min. This outflow of cool, moist air at the lower entrance enabled the salamanders to occupy crevices 15 ft outside the entrance.

9. The visible population in each cave was high at the initial count in June, dropped during July, and remained at low levels until April, when the population numbers again increased to a point comparable with the initial count. This population cycle may have been due, in part, to moisture conditions within the caves, resulting from lower than normal precipitation in the area of study.

10. The effect of man's disturbance on one population of cave salamanders and the resulting change in numbers and population structure is described.

11. The animals were marked by toe-clipping in order to determine from the recapture data population size and distances moved. Of the 141 salamanders marked during the study in all four study caves, 31 (26.7 per cent) were recaptured. Percentage of recaptures ranged from 16.7 in Tawney's Cave to 33.3 in Lucas Cave. Estimates of the population size in each cave by the Lincoln Index method gave the following results: Lucas Cave, 62; Williams Cave, 60; Link Cave, 63; Tawney's Cave, 36.

12. Male salamanders outnumbered females in a ratio of 1.51:1.00. No obvious reason for this numerical superiority of males was found. The monthly changes in sex ratio show the largest percentage of males during September and October, a time when most females were gravid. Juveniles composed 11.35 per cent of the 141 animals marked.

13. Analyses of stomachs from thirteen *E. lucifuga* and ten *E. longicauda* show that both species eat the same type of food, apparently any insect or any other animal that falls within the proper size range.

14. The possibility of competition between *E. lucifuga* and *E. longicauda* is discussed. This possibility is based on the low frequency of co-occurrence of the two species and their similar ecological requirements.

15. Dehydration experiments show that *E. lucifuga* has an average vital limit of water loss of 27.7 per cent of the total body weight and *E. longicauda*, 11.7 per cent. These results indicate that *E. lucifuga* is able to inhabit a dryer environment than is *E. longicauda*.

16. No significant differences were found in the critical thermal maxima of *E. lucifuga*, *E. longicauda*, or *Aneides aeneus*.

17. Activity was studied by means of a recording apparatus in order to determine if periodic activity occurred in *E. lucifuga* or *E. longicauda*. *E. lucifuga* showed only arrhythmic movements, but *E. longicauda* showed a definite period of activity, usually lasting about two hours and beginning from 7 o'clock to 10

o'clock in the evening. This difference in activity is supported by field observations.

18. The reaction of *E. lucifuga* to light was determined experimentally by giving individuals a choice of a dark side and a lighted side of a box and by subjecting groups of animals to an artificial light gradient. Results indicate that *E. lucifuga* is only slightly negative in its photic reaction.

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BIOTIC ASPECTION IN THE COAST RANGE MOUNTAINS OF NORTHWESTERN OREGON*

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INTRODUCTION

From the fall of 1932 to the spring of 1938, the author conducted an ecological investigation of a Douglas fir-hemlock community in the Coast Range Mountains of northwestern Oregon. Biotic and environmental observations, collections, and instrumental data were recorded weekly within a restricted portion of the forest. Information was obtained on the fundamental structure, organization, and interrelationship of animal communities in a typical forest of this area. This paper, however, will concern itself only with an aspectional interpretation of the data secured.

Acknowledgment is made to the late Dr. R. H. Wolcott, for suggesting the project, and to Dr. I. H. Blake for his guidance. The University of Nebraska, the Pacific Northwest Forest and Range Experiment Station, and Linfield College loaned equipment and the college also provided the services of research assistants. Tektronix Inc. of Portland, Oregon gave generous financial assistance for completing this publication. The continuity of this study resulted from efforts of many individuals, several of whom were unpaid. D. McKey-Fender has been the chief contributor to the compilation and editorial phases and Mary Comber Miles deserves credit for the graphs, charts and photographs.

Determinations of specimens were made by the following authorities: C. P. Alexander (Tipulidae); L. C. Altman (Megascolecidae); F. C. Baker (Mollusca); Wm. W. Baker (Rhynchophoridae); Nathan Banks (Acarina, Phalangida, Psocidae, and Mecoptera); R. H. Beamer (Cicadellidae); W. A. Bell

(Enchytraeidae); Bernard Benesh (Lucanidae); J. Bequaert (ectoparasites, Leptidae, Tabanidae, and Vespidae); Adam G. Boving (coleopterous larvae); F. M. Carpenter (Neuroptera); J. C. Chamberlain (Pseudoscorpionida); R. V. Chamberlain (Myriapoda); Q. D. Clarkson (spermatophytes); J. A. Comstock (Macrolepidoptera); J. F. Gates Clarke (Microlepidoptera); S. E. Crumb (lepidopterous larvae); C. H. Curran (Diptera); R. A. Cushman (Ichneumonidae); Kathleen C. Doering (Cercopidae); John Davis (Cicadellidae); E. O. Essig (Aphididae); E. P. Felt (Cecidomyidae); M. H. Hatch (Staphylinidae); Kenneth M. Fender (Coleoptera and Lepidoptera); Geo. R. Ferguson (Serphoidea); T. H. Frison (Plecoptera and Apidae); Harriet Exline Frizzell (Araneida); A. B. Gahan (Chalcidoidea); C. M. Gjullin (Culicidae); C. T. Greene (dipterous larvae); Kenneth Gordon (Amphibia); A. B. Gurney (neuropterous larvae); Carl Heinrich (lepidopterous larvae and Microlepidoptera); Ralph Hopping (Coleoptera); T. H. Hubbell (Rhaphidophorinae); H. G. James (Collembola); S. G. Jewett (Mammalia and Aves); H. H. Kieffer (Microlepidoptera); Karl V. Krombein (Sphecidae); M. C. Lane (Elateridae); Hugh B. Leech (Staphylinidae); S. F. Light (Isoptera); E. G. Linsley (Andrenidae); J. O. Maloney (Isopoda); D. McKey-Fender (spermatophytes and miscellaneous invertebrates); C. F. W. Muesebeck (Aleyrodidae, Ichneumonidae, and Braconidae); G. Riegel (Braconidae); E. S. Ross (Histeridae); H. H. Ross (Trichoptera, Tenthredinidae, including larvae); V. D. Roth (Araneida); H. C. Severin (Orthoptera); F. R. Shaw (Fungivoridae); James R. Slater (Amphibia); H. R. Smith (Formicidae); Roger C. Smith

*Studies from the Department of Zoology, University of Nebraska, No. 299.

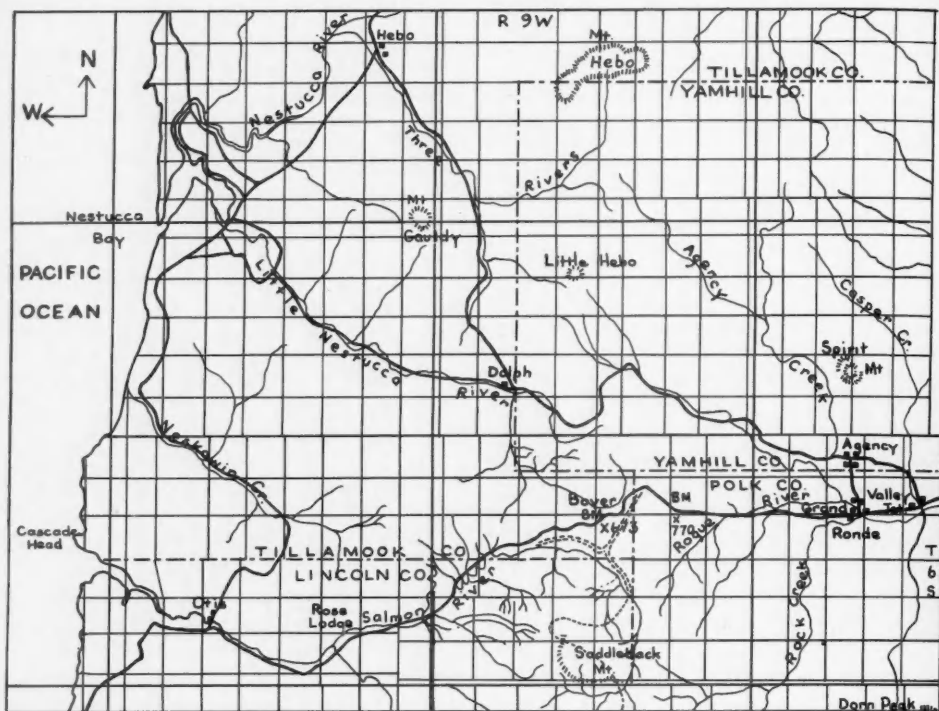


FIG. 1. Map of region, adapted from Forest Service map of Hebo Ranger District, Siuslaw National Forest.

(Neuroptera); T. E. Snyder (Isoptera); G. Spencer (Thysanura); L. H. Weld (Cynipidae); A. Wetmore (dipterous larvae); Katherine A. Wolfe (mosses); and E. P. Van Duzee (Hemiptera).

Accuracy of the account of the geology of the region was very kindly checked by Ralph S. Mason of the Department of Geology and Mineral Industries of the State of Oregon and Ruth Hopson of Portland State College.

DESCRIPTION OF AREA

The site studied was located in the southwest quarter of Section 24, Township 6 south, Range 9 west in the extreme northeast corner section of Lincoln County, Oregon. The area was on a terrace-like ridge sloping gently toward the north from Saddleback Mountain, which is a basic igneous intruded mass. Saddleback is one of the more massive mountains of the Coast Range, the bulk of the mountain proper occupying more than two sections. It lies in the adjoining corners of four topographic maps, the Nestucca Bay, Spirit Mountain, Euchre Mountain, and Valsetz quadrangles, the ridge on which this research was conducted being in the southwest corner of the Spirit Mountain quadrangle. This mountain appears as Saddle Mountain on Forest Service maps and is called Saddlebags locally, distinguishing it from the well known Saddle Mountain in Clatsop County as well as other mountains of the same name. Its elevation is 3359 ft above sea level, while the research area,

which became known as "the station," was located at an elevation between 1400 and 1500 ft. The instruments were situated, and most of the observations and collections were made, at about 1420 ft. The area was only accessible by a trail which extended from Boyer southwestward approximately 4 mi to the study area and thence to the top of the mountain. Boyer was a service station situated 6 mi west of Grand Ronde on the Salmon River Highway, i.e., Oregon 18 (Fig. 1).

GEOLOGY

According to Souza (1927), the Coast Range of Oregon consists of gentle, truncated folds trending generally to the northeast, the relationships of which are such as to constitute an anticlinorium. The very regular level to which the mountains have been eroded, averaging 1500 ft, can be explained by normal processes of erosion in the well-developed stream system characteristic of this humid region. Igneous intrusions in the form of sills and dikes have been important in the history and physiography of the region. Saddleback Mountain, as well as Mount Hebo to the north (Fig. 2), owes its height to the protection of a thick cap of gabbro over the softer sedimentary strata (Baldwin & Roberts 1952). The ridge on which the study was made, together with other spurs to the east of the station area, ends abruptly in a steep slope extending down to the Salmon River and its tributaries, which lie in a low, broad valley or pass

traversing the Coast Ridge, geologically a shallow fault trough. It was through this low pass at a maximum elevation of 730 ft that the Salmon River Highway was constructed only 2 yrs before this study was begun. While the silhouetted profile of the ridge very much resembles that of an uplifted sea terrace, its contours are explained by the presence of a rather thick dike at about the level of the research station (Fig. 3). It is this dike and attendant faulting that forms the southern scarp of the pass referred to above. The contours of this scarp are much softened by erosion, and at the time of this research were clothed in forest.



Fig. 2. View from near summit of Saddleback Mt. toward north, showing the topography of the Coast Range Mountains and the nature of the forest cover of this region. View is directly across the gap through which the Salmon River highway runs. Mt. Hebo, whose geological relationships are similar to those of Saddleback, can be seen in the middle distance. Photo by Howard Daniels, April 8, 1934.

SOIL

The soil was rusty-brown in color and of a crumbly texture on the surface. The darker surface layer extended to a depth of 4-6 in., below which a lighter brown or dark yellow silty clay subsoil of considerable depth was encountered. Pits of 1.5-2.0 ft in depth were dug without striking parent rock beneath. Probably in this location the depth of soil had been augmented by washing and sliding of material from higher levels over the top of the decomposed residual soil.

The soil apparently belongs to the pedalfer group and is an imperfectly podzolized type originating from basic volcanic rock. Large boulders are found scattered throughout the soil and on the surface. The soil survey of Yamhill County, Oregon, places this type among the brown or rusty-brown soils of the Olympic series (Koehler 1920).

HISTORY

The influences of civilization upon the Saddleback Mountain area had not been extensive up to the time of this research. Previous to 1910 apparently the only disturbing factors were visits to the region by trappers and hunters. Probably few, if any, permanent shelters or buildings were erected and no clearings were made. A square of logs may be seen in the eastern part of the hectare illustrated in Figure 4 which may be the foundation of a shelter, or more

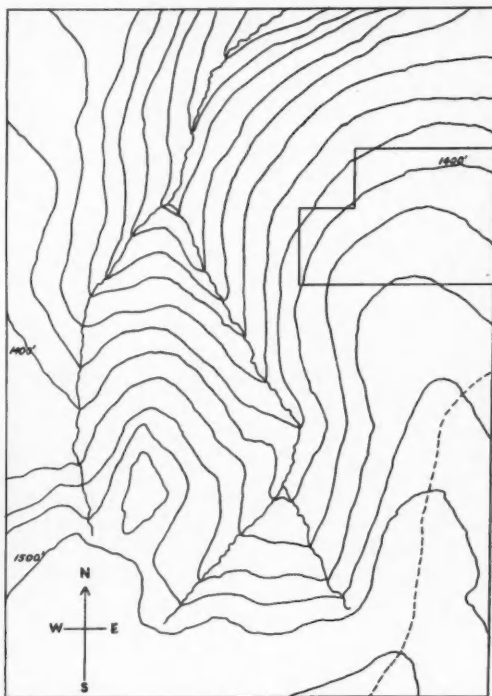


Fig. 3. Contour map of the research area. Contour interval equals 25 ft. Area enclosed in heavy lines is reproduced in detail in Figure 4.

likely a bear trap belonging to this period. About 1910 this territory was opened up to those desiring to file on timber claims. Many clearings were made, each of an acre or two in extent, in which cabins and barns were erected. At least 5 or 6 of these clearings were within 1 mi. of the research station. A road over which freight was hauled to the cabins extended up the mountain and ended about a quarter of a mile above the station. After the road was abandoned, it served as a pack trail, which wound up the mountain, crossing the ridge on which the station was situated a few hundred yards south of the research area. During the short period when timber claims were being established, the district was fairly well populated and the effect of trapping and hunting on wild life was undoubtedly marked. It was probably at this time that the few martens remaining in the area were eliminated, as well as elk herds that used to roam over the district.

About 1912 the timber claims were abandoned as dramatically and suddenly as they had been taken up. Cabins were left almost intact by their owners. In many instances the sheds were full of fuel wood, some provisions were left, and much household furniture remained. The owners had been handsomely rewarded by the sale of their timber to large logging companies such as the Miami Logging Company of Grand Ronde, Oregon, and others. The new owners sent in

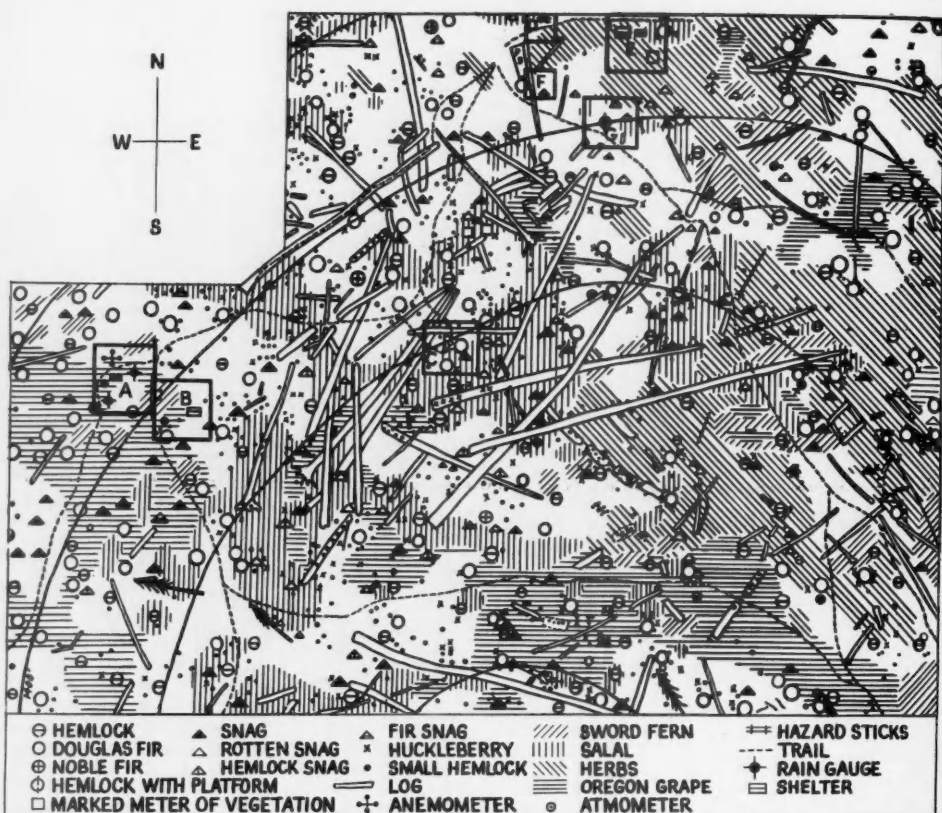


FIG. 4. Vegetation map of the area studied intensively, restricted research area (about $1\frac{1}{4}$ hectares) being shown in considerable detail. Symbols indicate type and extent of the vegetation (see key below map). Each study location is designated by letter and enclosed by heavy lines. (Orientation in relation to larger research area is shown in Fig. 3.) Adapted from Dirks, 1941.

crews to destroy some of the cabins and discouraged hunting or trapping in the area for fear of fires. Trails and roads were allowed to become blocked by fallen trees and soon became overgrown with salmon-berry bushes and bracken fern. This in itself discouraged travel in the region, and the primeval wilderness soon reasserted itself. Due to the resultant inaccessibility, the area proved to be an ideal location for ecological research.

The vegetation was practically untouched. Clearings of the settlers had largely grown up into young hemlocks, firs, bracken fern, salal, and salmon-berry bushes. Aside from a few hunters in the fall, a few fishermen, and an occasional trapper or timber cruiser, the area was undisturbed. Even these intruders confined their activities largely to the main trails and water courses, as is evidenced by the fact that no instruments used in this research were molested until the last week of the investigation.

VEGETATION*

At the time of this investigation, virtually the en-

* Terminology of higher plants throughout this paper is after Abrams, *Illustrated Flora of the Pacific States*.

tire area was covered by coniferous forest. There were occasional large natural openings occupied by a rank growth of bracken fern (*Pteridium aquilinum pubescens*), salal (*Gaultheria shallon*), and thimbleberry (*Rubus parviflorus*), and the small clearings made by settlers were filled with young trees and shrubby vegetation. The forest consisted primarily of an even-aged canopy of Douglas fir (*Pseudotsuga taxifolia*) with an understory of hemlock (*Tsuga heterophylla*) of varying ages. Occasionally at the 1400-1500 ft elevation isolated noble firs (*Abies nobilis*) added some variety to the canopy and very rarely a spindling broadleaf maple (*Acer macrophyllum*) was added to the understory. At the elevation where the instruments were located and the major part of the collecting done, a count was made of tree rings on stumps after the area was logged off, in 1939-40. The Douglas fir averaged approximately 250 yrs in age and two stumps of noble fir were the same age. The larger hemlocks varied from 95 to 270 yrs. This would indicate that no large forest fires had occurred here for at least that length of time, which was borne out by the lack of fire scars on the trees or in the

stumps. Across a ravine to the west many of the trees were much younger, as a fire had burned most of the larger timber some 50-100 yrs previously. The date was not established.

In the immediate vicinity of the research station the large Douglas firs and noble firs formed a canopy at an approximate height of 250-300 ft with the lower living limbs located at about 150 ft. The diameter of the trunks at breast height averaged 4 ft. The larger hemlock trees formed an understory with their first live branches usually beginning at a height of approximately 75 ft and the tops reaching up to the level of the lowest living Douglas fir limbs at 150 ft (Fig. 5). This timber was somewhat past its prime and every year took toll of a few giant firs or hemlocks which had been weakened by fungus and were blown over in a storm. These fatalities left openings in the canopy and eliminated root competition enabling a second generation of hemlocks to gain a foothold. This second understory was very irregular in height and size of trees. Some of the largest were tall enough to reach up to the lower, large hemlock limbs and had a d.b.h. of 1 ft or more. Others were mere seedlings. Figure 4 shows these trees scattered more or less throughout the area but concentrated along the summit of the ridge. There they formed such a dense understory that the surface of the soil was barren of all herbaceous and shrubby growth.



Fig. 5. View from the south showing Location G (the "high hemlock") and environs during the hibernine sector. Ladder on the trunk of the large hemlock may be seen in the central background leading to the platform at an elevation of 80.5 ft (upper center). Photo by Charles Sanford, Feb. 6, 1937.

Associated with the small hemlocks, but also scattered elsewhere throughout the area, were shrubs about 3-10 ft tall. Most of the taller ones were red huckleberries (*Vaccinium parvifolium*). There were also several dense patches of salal from 8 or 10 to a maximum of approximately 50 ft in diameter and about 3 ft in height. A few very weak and inconspicuous vine maples (*Acer circinatum*) were also present (Fig. 6).

Where the upper canopy was more continuous and young hemlocks and large shrubs therefore largely absent, the soil supported a scattered growth of the ever-



Fig. 6. General view of forest in autumnal aspect showing red huckleberry, vine maple and sword fern. Douglas fir at right measures 3 ft d.b.h. Picture taken Sept. 19, 1954, in Van Duzer Wayside State Park, an area a few miles distant, but typical of the study area before it was logged. Photo by Howard Daniels.

green Oregon grape (*Mahonia nervosa*) and sword fern (*Polystichum munitum*).

In the spring and early summer the herbaceous layer appeared, including a rather dense growth of vanilla-leaf (*Achlys triphylla*) with more scattered specimens of false Solomon's-seal (*Smilacina sessilifolia*), wild lily-of-the-valley (*Maianthemum dilatatum*), fairy bells (*Disporum smithii*), cool-wort (*Tiarella trifoliata*), *Trillium ovatum*, and wood-rush (*Luzula parviflora*). Patches of *Clintonia uniflora* and *Oxalis oregana* formed carpets, and where the sun could penetrate, violets (*Viola sempervirens*), tway-blade (*Listera caurina*), *Dentaria tenella*, and *Moneses uniflora* were throughout the area. Even under the dense shade of the young hemlocks an occasional saprophytic orchid (*Corallorhiza mertensiana* and *C. maculata*) might be found and more rarely a specimen of Indian pipe (*Monotropa uniflora*) (Fig. 7). Mosses (*Rhytidiadelphus loreus* (L.) Hedw. and *Hylocomium splendens* (Hedw.)) covered the logs, the bases of tree trunks, upper surfaces of fallen limbs, and carpeted the ground wherever other vegetation was not too dense (Fig. 8). The only place where they were absent was in the densest shade of closely growing young hemlocks.

Covering the soil was a litter and humus layer, which in most places approximated 2 in. in thickness, and consisted of needles and branches in all stages of decay, bound together by fungal threads. Where an



FIG. 7. Detail of herb layer in the serotinine sector of the autumnal aspect. Picture taken Aug. 15, 1954, 15 yrs after the area had been logged, yet typical of much of the area at the time it was studied. Plants include *Oxalis*, *Trientalis*, vanilla-leaf and sword fern. Twigs of a small hemlock appear at upper border and a small salal appears at right. Photo by Howard Daniels.



FIG. 8. Detail of ground stratum showing mosses, chiefly *Hylocomium splendens* (Hedw.). Typical of north part of Heetare 17 (Fig. 4). Photo by Howard Daniels, Sept. 19, 1954.

old snag or log had decayed, this humus layer would be as much as 6 in. or even more in depth.

CLIMATE

The climate of the Coast Range mountains is extremely humid. According to Wells (1941), "There are some localities on the west slope of the Coast Range (in Oregon) that have heavier precipitation than has been recorded in any other State except in some corresponding areas in Washington. . . . In general precipitation increases from the coast to a belt near the summit of the Coast Range." This location, while exposed to the direct sweep of fog and rain-bearing winds from the Pacific Ocean, did not show an annual precipitation as high as reported for areas farther north on the Coast Range, partly be-

cause rain gauges sometimes ran over during heavy mid-week storms. Nevertheless, average recorded annual precipitation was in excess of 89 in. It is a country of very wet winters and dry summers. Most of the precipitation at this level falls in the form of rain. Snow is seldom very deep and usually does not stay long except on the summits of the mountains. Some winters there is practically no snow. An appreciable amount of precipitation occurs in the forest in the form of "Nebel-reisen" or horizontal precipitation caused by condensation of moisture on trees from saturated winds. This drips to the ground beneath and often wets it when outside the forest the soil and vegetation are perfectly dry.

Most of the moisture falls from October to April borne by moisture-laden winds from the southwest or west. These winds are usually light to moderate, but occasionally lash the coast and mountains with such fury as to flatten the more weakly anchored forest trees, and the accompanying floods of water turn streams into raging torrents. Northeast winds are more prevalent during the summer and bring the humidity down abruptly. They generally do not blow for many days at a time, but even in the winter cause the forest to become decidedly dry on the rare occasions when they continue for a week or two. Northeast winds also bring subnormal to freezing temperatures in the winter and abnormally high temperatures in the summer. The wind velocity is greatly reduced within the forest but the accompanying humidity and temperature produce very definite changes in the environment of the forest floor. Wind velocity seldom averages more than 50 mi/day, as recorded by an anemometer at low shrub level, even in the highest gales.

The temperature of this region is famed for its moderation. Within the forest this characteristic is even more evident than in open areas. The average mean temperature for 4 yrs. at this location was approximately 50° F. Temperatures above 70° were very rare and the maximum recorded temperature was 89° F. On the other hand, low temperatures were just as rare. No temperatures close to zero were encountered, the lowest being 11° F. Often when the soil was frozen hard outside the forest, no signs of freezing would be found upon entering the timber. The soil rarely froze beneath the trees. Low temperatures within the forest were usually accompanied by a snowfall or a glaze of sleet. Occasional freezing periods without snow were produced by a strong northeast wind. In the fall the temperatures at this elevation remained considerably above those in the valleys until late in the season, while in the spring, temperatures on the mountain lagged behind those in the lower, open country.

METHODS OF STUDY

Observations, collections and instrumental records were taken weekly from September 18, 1932 to January 9, 1938. A preliminary reconnaissance covering several sections of forested land was con-

ducted to find a suitable location in mature timber. This survey was based on data gathered from County Assessors' offices, from local residents, and from the Pacific Northwest Forest and Range Experiment Station in Portland, Oregon. During this period, field records were kept of all faunal activity and some invertebrates were collected. The vegetation was studied with special care. Information concerning timber cruises, section corner locations, old cabin sites, etc., was checked in the field before a definite location was selected. This phase of the work occupied from September 18, 1932 to February 25, 1933.

INSTRUMENTS

January 21st, 1933, observations were started on the ridge about one-eighth of a mile above the restricted area finally selected for study. On that date a maximum-minimum thermometer was set up 5 ft above the ground level on the north side of a large Douglas fir tree where it remained until June 3, 1933. On February 25th, 1933, a Friez hygrothermograph, an anemometer, and a cylindrical atmometer were installed at the research station. On March 4th, two Forest Service rain-gauges and a set of maximum-minimum thermometers were added, thus completing the battery of instruments installed in the early phase of the study.

At the beginning of the project, the plan was to use stratal data, hence instruments were distributed through as many strata as possible. One of the principal strata was formed by a canopy of Douglas fir crowns 250 ft or more in height. However, the equipment necessary to sample this stratum adequately was unobtainable. Instruments were placed at seven minor locations which have been designated in the order of their establishments at A, B, C, D, E, F and G. These locations are indicated in Figure 4.

The area occupied by Locations D, E, and F lay east of the grove of young hemlocks, on the summit of the ridge, in open timber free from tall shrubs, young trees, or other undergrowth. It was even comparatively free from low shrubs or herbs, and the soil was generally covered with a light growth of mosses over the needles and twigs. This area was exposed to the morning sun and north, east, and south winds, but was protected to some degree from the afternoon sun and west or southwest winds by the young hemlock stand. It was in this vicinity that most of the collections and observations were made.

A fire shelter (FS, Fig. 4), or lean-to, facing west, in front of which fires were built in cold weather, was located about 150 ft northeast of Station C (Fig. 9). Location D was established 20 ft farther north down the ridge where hazard sticks were set up at a level 6 in. above the soil surface, among sword fern and vanilla-leaf and on the east side of a large Douglas fir tree. Location E was 60 ft east of the lean-to and at the same elevation. An instrument shelter was erected to enclose the Taylor recording thermometer, the bulb of which was buried near by, 2 in. beneath a heavy carpet of moss covering a low mound, the re-

sult of an old windfall. At location F, Wynne photometer readings were made at an elevation of 3.5 ft, by placing the instrument 4 ft south of the fire shelter on a log which supported that structure (Fig. 4).



FIG. 9. View toward east from in front of the fire shelter during the vernine sector, showing the open character of the forest in this study center. Locations E (thermograph shelter) and F (site of photometer readings) are indicated by letters. Location G is hidden by the large Douglas fir to the right of the shelter, while the herb quadrat at Location E is obscured by the left-hand corner of the fire shelter (see Fig. 4). Photo by M. R. Edmunds, Apr. 24, 1935.

COLLECTING METHODS

The data from the soil layer have not been included in this paper. Regular quantitative counts and surface observations of the humus and moss layer were made over areas which varied in size, depending upon the abundance and size of specimens.

The shrub layer was sampled by a number of methods, each of which produced good results for some part of the population. Random sampling was carried on regularly by means of sweep nets of various sizes and by individual hand-picked collections, in an attempt to obtain representative specimens of the common animals for identification. The specimens were counted in the net after being killed or immobilized by placing the tip of the net for a few minutes in a large cyanide jar. A third method was that of beating the shrubs over 1 sq m of canvas held horizontally by crossed sticks inserted into pockets in the corners. Specimens were then picked off the canvas before they could run or fly away. This was especially successful in obtaining spiders and slow-moving insects on cool days. A fourth method was that of closely examining marked square meters of vegetation for a given length of time—usually about 15 minutes. No collections were made from these marked quadrats.

The low hemlock layer was sampled by all of the methods enumerated for the shrubs and herbs. The beating method was most satisfactory in this layer. Collections were also made of insects lighting or flying across the low hemlock platform.

The high hemlock layer was sampled least successfully. Random collections were made from the bark and boughs, as well as on the platform. Also, some aerial counts were made. A sweep net was used but only random collecting was possible.

The rotting logs, snags, stumps, and other down timber were sampled by examining at random and by collecting and counting specimens over a certain area.

For amphibia, pitfalls were found to be an effective method of collecting. These were formed by smoothing the vertical sides of pits made in using the soil-sample counting chamber. Birds were studied by noting their various calls and by estimating the size of flocks or number of nests over a given area. A few specimens were shot outside the area for specific determination. Small mammals were caught by snap traps placed in runways, near holes, and by stumps, logs, or in other favorable locations. Poisoning was tried off the area but with little success. Molehills and runways were counted over a definite area. Tracks, "sign" and other evidences were used to obtain information on larger mammals.

In addition to collections and observations over this restricted area, regular observations and some collections were made along the trail each week during the trip to and from the research station. Since these were, for the most part, at a lower elevation, they were not strictly comparable with results at the station but produced a good deal of supporting evidence from the aspectional standpoint. Occasional trips were also made to the top of Saddleback Mountain for additional information and observation.

Soft-bodied specimens were preserved in alcohol. Insects were put in vials, pillboxes, or cellophane envelopes to be transported to the laboratory where they were sorted, pinned, and sent to specialists for identification. Amphibia were taken to the laboratory alive where they were killed and preserved in alcohol and formalin. Birds and mammals were shot or trapped, measured, and study skins made for identifications. Their stomach contents were regularly preserved.

A survey was made of the area used for this investigation. Starting from the southwest section-corner, the area intensively investigated was divided into hectares and contour lines were run at 25-ft intervals as shown in Figs. 3 & 4. The hectare corners and contour lines were marked with white and colored rags so that collections could be definitely located as to elevation and hectare. Hectare 17, which included Stations C, D, E, F, and G, was divided into dekameter squares to permit even more accurate location in this area. Hectare 17 and part of hectare 16 were then mapped for location, distribution, and types of vegetation, as shown in Fig. 4.

ASPECTION

HISTORY AND CRITERIA

Aspection may be defined as the seasonal rhythm of the presence and activities of conspicuous organisms

within a community. It is equivalent to *seasonal succession* (Allee *et al.* 1949). Aspection as a phase of ecological interest has not attained the degree of importance which it deserves. In the field of botany it enjoyed a period of popularity under the term *phenology*. In the latter part of the 19th century, a number of articles were published on the development of buds, leaves, flowers, fruits and defoliation of trees. Some of the early publications on phenology also considered the seasonal effects on animals (Hough 1864, Robertson 1895). Also there were attempts to correlate phenological and meteorological phenomena (Mikesell 1883). This phase of interest in seasonal phenomena reached a high point in the "Calendar of Leafing, Flowering, and Seeding of the Common Trees of the Eastern United States" (Lamb 1915). Hopkins & Murray (1932), on the basis of a few selected woody plants, established botanical criteria that have been utilized in a number of ecological studies. Shelford (1929) applied the term phenology to the study of correlations between periodic phenomena exhibited by plants and migrations of animals and birds. In 1935, the committee on nomenclature of the Ecological Society of America defined phenology as that science that deals with the time of appearance of characteristic periodic events in the life cycles of organisms under natural conditions, especially those influenced by temperature, latitude and altitude, among other influences in the physical environment. Thus, the term phenology has taken on a wide meaning, the terms "phenological" and "seasonal" being considered equivalent. Huberman (1941) summarized North American phenological efforts, classifying studies in three groups: the construction of calendars and charts without regard to meteorological factors, the correlation of plant and animal activities with meteorological factors, and the applications of the principals of bioclimatology. Glendenning (1943) has termed phenology "the most natural of sciences" and pointed out the value of seasonal studies. During the last decade, several notable phenological studies have appeared, one of the most comprehensive being that of Leopold & Jones (1947), in which were tabulated and analysed 328 seasonal events during the decade 1935-1945 in Wisconsin. Phenological observations have found practical applications in a number of recent studies such as those of Costello & Price (1939) on determining grazing periods on mountain range, Lathrop & Dirks (1944) on timing the seasonal cycles of insects and Penfound *et al.* (1945) on mosquito control. Elsewhere in the world, studies of seasonal phenomena under the term phenology have experienced a mild resurgence in recent years. Among such works may be cited those of Batista Diaz (1942), Rosenkranz (1947, 1948), Marcello (1947, 1950), Voigts (1949), Ledesma (1949), Kurauchi (1951), Kontkanen (1950), Linnavuori (1952) and the reports of phenological observations in the British Isles appearing in the Quarterly Journal of the Meteorological Society, London (*e.g.* Gunton 1943). Many if not most of these works appear to be of a practical nature.

Interest in aspection among North American ecologists originated with Pound & Clements (1898), who recognized "a vernal and an aestival-serotinal aspect" in the prairie. These authors later expanded their concept of seasonal societies, for Wolcott (1918) refers to Pound & Clements' (1900) division of the flowering periods of plants into prevernal, vernal, estival and serotinal aspects. In botanical ecology, the study of aspection was long restricted to the description of seasonal or aspectional societies indicated by the conspicuous subdominant flowering plants of the various seasons. This concept of aspection probably reaches a climax in the description of the seasonal aspects of the prairie by Weaver & Fitzpatrick (1934) who indicated approximate aspectional dates for prevernal, vernal, aestival, autumnal, and hial societies but gave no correlation with specific environmental data. Wolfe *et al.* (1949) established botanical criteria based on both floral and vegetational phenomena, and correlated with environmental factors. This study has invited use and commentary by others, notably Cantlon (1953) who studied vegetation and microclimates as particularly applied to topography. Ellison (1954) dates aspection in subalpine vegetation in terms of days from snow melt.

Zoologists have also made numerous contributions to the fund of aspectional information. Adams (1913) noted in his bibliography seasonal succession as recognized by European naturalists. In the same year, Shelford (1913) gave a brief account of seasonal succession, citing definite dates of observation. Wolcott (1918) wrote on seasonal changes in southeastern Nebraska, stressing the correlation of specific physical factors with the biotic phenomena represented in the four seasons of spring, summer, fall and winter. He indicated that environmental and biotic evidence would start these seasons about two or three weeks ahead of the astronomical dates for seasonal limits and pointed out faunal evidences of seasonal activity.

This introduction to faunal aspection was followed by publications of Shelford (1918) and Sanders & Shelford (1922) on seasonal occurrences in animals. Weese (1924b) recognized the adjustment of characteristic insects in a deciduous forest to climatic rhythm and the effect of environmental factors of moisture and temperature in stimulating seasonal migrations. In 1928, V. G. Smith published a definitely dated list of seasonal "societies" for a deciduous forest community in which she recognized vernal, aestival, serotinal, autumnal and hial societies. This paper represented the first attempt at organization of an entire fauna, from an aspectional standpoint, through a complete annual cycle. The data were graphically represented in a cyclic arrangement, but no attempt was made to correlate the seasons with environmental fluctuations. This was followed by the report of Shackleford (1929) in which environmental factors were considered, in addition to the fauna, through the various seasons of an annual cycle.

Subsequent faunal investigations by animal ecologists have shown a tendency to recognize seasonal

societies as a definite part of the community structure. Bird (1930) listed seasons for two successive years in the aspen parkland of Canada, based on the fluctuating animal population, with special emphasis on the vertebrates. Davidson (1930) listed definitely dated seasons without indicating any precise basis for their determination. Brown (1931) compared the seasons in Missouri and Oklahoma oak-hickory forests showing a correlation of the curves of animal population with temperature and precipitation. Seasonal societies also were emphasized in the faunal investigations of Davidson (1932) and Shackleford (1935). In 1936, four ecological publications appeared, all of which recognized the aspectional distribution of the fauna. Carpenter (1936a, b) suggested that the winter population might be divided into hial and hibern societies (societies). Daubenmire (1936) dates the seasons for the "big woods" of Minnesota, and Williams (1936) gave an excellent description of aspectional changes in a beech-maple climax community. Williams included not only faunal population changes but correlated these with floral aspection and environmental changes, as well as with altered physiological activity of faunal inhabitants. His work apparently was based chiefly on general observation of environmental phenomena, as no instrumental records were reported. Carpenter (1939) considered aspection on a mixed grass prairie in Oklahoma, including observations of both plants and invertebrates, and Shackleford (1942) also worked in Oklahoma, designating the seasons as expressed by invertebrate populations of herbs in poorly-drained, overgrazed grassland. McClure (1943) wrote on the biotic communities of the Churchill area, Manitoba, basing his concept of aspection upon the flowering dates of plants. He gave population records for the fauna, as well as environmental records, which could be correlated with the plant aspection, but no definite seasonal societies were delineated. Twomey (1945), in a study of the bird population of an Illinois elm-maple forest delineates seasons, using meteorological records as well as faunal and vegetational data. Dowdy (1944) found that seasonal concepts held for invertebrates in disturbed forest in Ohio and described (1950) the seasonal features of stratal societies in an oak-hickory association. Jones (1946) considered the effect of climate upon aspection and annuation in an elm-maple forest in Illinois (the same woods studied by Twomey 1945). Dirks-Edmunds (1947) included aspection and annuation in a comparison of biotic communities in Illinois oak-hickory and Oregon Coast Range cedar-hemlock associations. Fichter (1954), in a quantitative study of invertebrate fauna of grassland and shrub savanna in eastern Nebraska, considered faunistic, floristic, and environmental expressions of seasonal concepts.

Thus we see the gradual growth and maturation of the aspectional concept, as recognized and used by American ecologists, from its beginnings in a purely floristic phenology, through recognition of faunal aspection, to correlation of seasonal phenomena with

environmental factors. Yet it seems probable that further refinement of seasonal concepts, criteria, and terminology is desirable.

As shown above, seasonal phenomena in plants and animals have long been recognized by biologists who have appreciated the fact that there were seasonal effects on living things that did not coincide with equinoxes and solstices, and that the activities of living organisms were the best indicators of such changes. Botanists have used the flowering of subdominant plants, usually confined to the herb layer, as the indicators of aspection or seasonal effects. This led to the use of the terms *hiemal* for winter, *vernal* for spring, *aestival* for summer and *serotinal* for fall seasons. Recently, *prevernal* has been used for a season of earliest blossoms and *autumnal* has been placed after *serotinal* as a late fall aspect.

With the exception of Wolcott (1918), who attempted to state exact limits of seasons by reference to temperatures, early investigators tended to express environmental criteria for seasons in rather general terms. Even yet, in few papers are seasonal criteria clearly expressed. In accord with the assertion (Vestal 1914) that the animal selects an environmental complex composed of three phases: physical, plant and animal, the author has attempted to designate the seasons by meteorological, botanical and faunal criteria.

ASPECTIONAL ANALYSIS

Fluctuations in faunal constituents were considered of prime importance in obtaining a picture of aspection in this community, although analyses of physical environmental factors, flora, and fauna have all been considered.

Population Changes

Many of the faunal collections were of a random character. It is therefore felt that the proportion of individuals of each species to the total population could not be accurately determined in an area including such varied and often comparatively inaccessible habitats and minor biotic communities, even though a representative sample of the common animals active at the time of observation was obtained. This was especially true of the vertebrates. Insects were the most abundant faunal group active in the community and were quite thoroughly collected and identified, hence the population has been analyzed from the standpoint of fluctuation in variety of insects. This procedure also follows the precedent set by Adams, Smith, Shackleford, Davidson and Brown. In determining the character of the total population throughout the year, or what might be termed the "faunal spectrum," an ideal record would be based on all species present in the habitat. In this project such an ideal could not be attained for several reasons. Some species could not be determined even by the specialists. It was often impossible in the field to differentiate similar species. Exact determination of every species was probably ecologically unimportant. Within a given family, related species more often than not

appeared to be biological equivalents, occupying much the same niches, using the same type of food, and often present during the same season of the year. For these reasons, and in order that there might be a definite basis for comparison with work of other investigators, the family was used as an arbitrary unit indicating variety of insect population. The total number of insect families collected or observed in the aerial strata of the community on each date the area was visited was calculated and graphed (Fig. 10, solid lines).

In addition to the above analysis of the insect population at the family level, compilation of the occurrence of common and conspicuous insects was made and their seasonal distribution tabulated. In order to be included in this phase of the population analysis, an insect must have been present on more than one of the collecting dates during the season in question for at least 3 out of the 5 yrs studied. While some of the species remain nameless because of the incomplete state of our knowledge of the fauna of the region, determinations are in general reliable and at the species level. (Tables 2, 4, 6, and 8, Fig. 15 and the columnar portion of Fig. 10 are based on the aforementioned data.)

One of the most obvious results of any analysis of the population is the recognition that certain species, or groups of species, suddenly become an integral part of the community while others dwindle to a position of unimportance or as suddenly disappear. This is occurring continually and gives rise to the feeling that the change in the complexion of the fauna from week to week is due to a gradual infiltration of new species and a gradual disappearance of others which in a relatively short time builds up an entirely different community structure. To represent the changing composition of the population a columnar graph was superimposed on the curve of population showing the number of distinctive and common insects appearing for the last time and the number appearing for the first time in each collecting period (Fig. 10). This not only indicates the expected continuous and gradual replacement of faunal units but also shows that on fairly definite dates an upheaval or turnover of animal species occurs producing a new faunal aspect as a result of new species being ushered into the active life of the community and others dropping out. As might be expected, the aspects that follow the winter period of low population are marked by a greater influx of new groups of insects than disappearance of those already present, while the aspects late in the summer are marked by more species dropping out than are added. Since either a decrease or increase of animals indicates a change, the sum of positive and negative results gives the total amplitude of change affecting the population. Because an exceptional waxing and waning of population indicates a surge in the even flow of the seasonal tide of population variety, such points appear to indicate the approximate seasonal limits. It is certain that a comparison of the fauna composing the population before

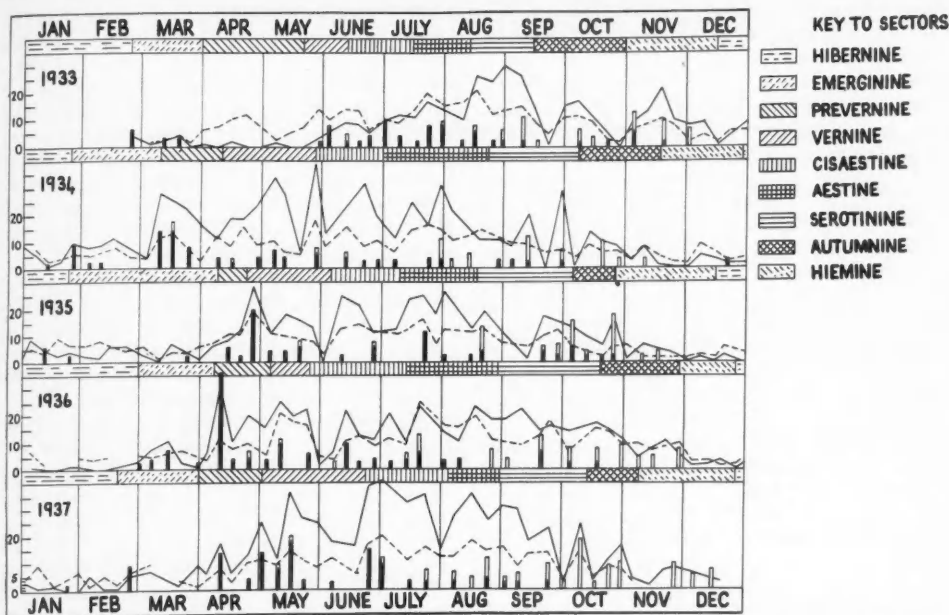


FIG. 10. Correlation of population and environmental factors. Solid line shows the number of families of insects active in the layers of the community above the soil surface on each collecting date: Scale—1 unit equals 1 family of insects. Broken line was produced by plotting a factor obtained by averaging the vapor-pressure deficit for time of observation, light intensity for that afternoon, and mean daily maximum vapor pressure deficit for the week preceding each trip: Scale—1 unit equals .020 of the environmental factor. Solid columns indicate the number of species of common insects appearing for the first time during the year on each date. Open columns indicate the number of species of common insects which appear for the last time during the year on each date. Scale—2 units equal 1 species. Seasonal limits are shown by shaded blocks on upper margin of each annual graph: key appears to the right.

and after one of these periods of fluctuation discloses an appreciable change in population structure. The boundaries of certain seasons for some years (e.g., vernal, 1935) seem to be sharply marked by a sudden change in the population, while in other years, the same season is not so clearly set off (e.g., vernal, 1934). Apparently these changes in population occur more abruptly in some years than in others. The most striking fluctuations occurred in 1937, either because collections were more consistent and more efficiently conducted in that year, or because a late spring shortened the active period. One possible weakness in the investigation that may have prevented the seasonal fluctuations from being more sharply defined is the psychological difficulty of making positive observations on negative phenomena. The dates on which animals became conspicuous by their absence were not consistently noted in the field records. If this information had been more carefully kept, it might have added somewhat to the height of the columns in the early seasons. As it is, these are marked chiefly by the appearance of new animals.

Correlation of Population with Environmental Data

The question that next arises pertains to the reason for such population differences as are shown in Figure

10. As a result of reviewing the effect of seasonal changes on animal life in the vicinity of Lincoln, Nebraska, from 1881 to 1917, Wolcott (1918) stated that the most obvious factor in seasonal changes is that of temperature. Further on he added, "Of the climatic factors (temperature, precipitation, sunshine and cloudiness, wind, humidity, soil moisture and barometric pressure) enumerated above, temperature and moisture have by far the most pronounced direct effect on animal life, not only in determining in a general way the character of the fauna of a locality but also in exerting a considerable control over the time of appearance of many species, as well as the abundance of many forms." Shelford (1913) states, "Seasonal succession is the succession of species or stages in the life histories of species over a given locality due to heredity and environic differences in the life histories (time of appearance) of species living there." The factor of heredity does not lie within the province of this investigation but that of "environic differences" does. Weaver & Clements (1938) emphasize the environmental factor, stating that seasonal aspects are determined primarily by the seasonal march of habitat factors, of which temperature and length of day are most important. Their conclusions deal primarily with plant life, in which length of

day has been demonstrated to exert a controlling influence, especially upon flower production. The gradual alteration of length of day is now known to have an effect upon animals (Allee *et al.* 1949) but has not been directly investigated in this study. Among fluctuating factors, the role of temperature is especially eligible for consideration. The direct effect of temperature is not its only effect. Sums of temperature have been shown to exert a controlling influence upon both plant and animal life (Artz & Ludwig 1949, Headlee 1941, Rosenkranz 1948). Besides temperature, Shackelford (1942) considered relative humidity, and to a certain extent precipitation, as factors influencing the occurrence of seasonal changes in invertebrate animal populations.

An inverse ratio between seasonal variations in animal population and variations in the evaporating power of the air in an elm-maple forest was found by Weese (1924). Brown (1931) also showed correlation of curves of animal population with temperature and precipitation in a deciduous forest. Adams (1941) reported, "The correlation coefficients indicate increases of animals with temperature increases and decreases with temperature decreases in all strata, and, in general, increases of animals with relative humidity decreases, or vice versa." He also considered the effect of evaporation but indicated no particular correlation.

The observation that the more modern, active insects tend to appear in environments of high energy intensity (midday, midsummer and the tropics) and the more primitive insects in environments of low intensity has been termed the Kennedy trend (Kennedy 1928). Whittaker (1952), in evaluating the application of this trend to various stations in the Great Smoky mountains, concluded that "the primary correlation of modernity is with the drying power of the atmosphere." On the basis of similar calculations for the Saddleback Mountain area, it was found that the highest modernity index of the year is in the early fall, which is also the season of highest evaporation and very low rainfall.

According to Shelford (1937), we are warranted in concluding that the evaporating power of the air is probably the best index of environmental conditions of land animals. The suggestion that as a measure of the evaporating power of the air vapor pressure deficits "are ecologically more significant than humidity values" was made by Weaver & Clements (1938). These authors refer to the work of Anderson (1936) in which the advantages of vapor pressure deficit measurements over relative humidity are summarized. Anderson concludes, "It is desirable that vapor pressure deficits be recorded in experimental work with organisms rather than relative humidities." Since vapor pressure deficit is the "difference between the saturation vapor pressure for the current temperature (dry bulb) and the saturation pressure for the temperature of the current dew point" (Weaver & Clements 1938), it is influenced by both the temperature and moisture content of the air. In addition An-

derson (1936) states, "Vapor pressure deficit alone does give an indication of evaporation rates." Anderson's statement has been criticized by Leighly (1937) who concluded that his analysis and conclusions were untenable and that evaporation is proportional, not to vapor pressure deficit, but to the vapor pressure gradient between the evaporating surface and the air. Thornthwaite (1940) enlarged upon this view and concluded that conventional methods of measuring atmospheric moisture were inadequate and attempts to correlate simple functions of atmospheric moisture were futile. Nevertheless, Huffaker (1942) found a correlation between vegetational distribution and vapor pressure deficit and relative humidity values in zonation of vegetation types in the United States, concluding that vapor pressure deficit provided a superior correlation, the general correspondence between vegetational and vapor pressure deficit lines being too great to be coincidental or even secondary.

Despite, or perhaps because of, the above conflicting views, it was decided to attempt vapor pressure deficit and population correlations in this study. It may be noted that in recent studies, others continue to use vapor pressure deficit values in biotic studies (*e.g.* Kucera 1954, Barnes & Barnes 1954).

Accordingly, vapor pressure deficits for the dates of collection were calculated and graphed from records taken at the low shrub level. The resulting curves were compared with the curves of population diversity shown in Figure 10. Correlation was apparent at once. As the vapor pressure deficit rose the variety of insects increased and as the vapor pressure deficit fell the number of insect groups usually became smaller. This curve was constructed from vapor pressure deficits calculated from hygrothermograph records for the time at which collections and observations were made. As a rule this was about 3:00 p.m. The vapor pressure deficit was usually quite stable during the afternoon while insects were most active; accordingly a figure selected for approximately the time of collection was representative.

At several points this correlation between vapor pressure deficit and complexity of faunal structure broke down. It seemed reasonable that perhaps the trend of vapor pressure deficit for the preceding week might in some cases exert an effect which would not be apparent when vapor pressure deficit for the time of collection was considered alone. Because the minimum vapor pressure deficit was very low for the entire year and fluctuated only slightly, it was not used. The mean daily maximum vapor pressure deficit for the preceding week, however, formed a curve with marked oscillations and these were of such a nature that in most cases, when averaged with the vapor pressure deficit reading at the time of collection, the resulting curve much more closely approximated that of population variability. A curve constructed from the mean vapor pressure deficit for the preceding week gave less favorable results because, while the graph was not materially changed, the fluctuations were too moderate to be effective. A final reason for

the use of the maximum reading is that a high vapor pressure deficit, through its correlation with greater environmental stress, would be likely to indicate a more stimulating effect on insect life in this environment than the mean vapor pressure deficit.

In a few points in the graph, even the use of the above-mentioned data did not produce as close correlation as might be desired. In casting about for an additional factor which could eliminate discrepancies it was discovered that the light intensity had an effect which would bring the environmental curve of vapor pressure deficit more nearly into line with the population curve. The light intensity, however, had to be determined from several sources. Wynne photometer readings were available at shrub level through most of the period from December 8, 1934, to June of 1937, and from October, 1937, to January, 1938. A Weston illuminometer was used during the summer of 1937. For the collecting dates on which no photometer or illuminometer records were available, weather observations were found to be consistent enough to provide a reasonable interpretation of the light intensity based on comparisons with similar days on which instrumental records were available. Since the photometric data were more extensive and were in terms of the percent of full sunlight, the illuminometer records and interpretations from type of day were reduced to the same basis of percentage.

To illustrate the procedure by which a combined factor was obtained by averaging the figures for the vapor pressure deficit and light intensity for the collecting date with mean maximum vapor pressure deficit for the preceding week, the following example is offered. On July 21, 1935, the mean daily maximum vapor pressure deficit for the preceding week was .332; the vapor pressure deficit for the collecting period was .287; and the factor of light intensity for that afternoon was 40% of full sunlight. Thus, averaging .332 plus .287 plus .406, a value of .339 is obtained. This calculation was performed for each collecting date. By comparing the type of environmental curve which would be produced on a graph, such as that shown in Figure 10, if only vapor pressure deficits were considered, with a graph in which a light factor is also averaged, the latter was found to conform more nearly to the population trend.

Even this combination of factors does not produce perfect correlation throughout. For many of the discrepancies, no adequate explanation can be advanced at present. Inadequate sampling of the population on some dates, undue emphasis on certain phases of the collecting, or environmental influences that escaped notice previous to the collection, can explain most correlation failures. Variation in skill of personnel assisting in the research on successive collecting dates accounts for poor correlation in the vernal aspect of 1934. When the temperature is low in the early spring and late fall and there is snow, the light intensity may be high, though the vapor pressure deficit on the collecting day is very low. This causes a comparatively high environmental curve to be main-

tained while at the same time the population curve drops to a low point. If the temperature is near the freezing point, even a bright sun, since it fails to reach many individuals below the canopy, is unable to produce much activity in the insect or arachnid population, while the physical effect of the snow is no doubt a deterrent to normal invertebrate activity. A situation of this kind is very clearly shown on November 2, 1935. On the other hand, on the last preceding collecting date, October 26, 1935, the light intensity was much lower, the vapor pressure deficit at the time of collection was somewhat higher, the temperature higher and the vegetation not extremely wet nor snow-covered. The environmental factor plotted for October 26th does not differ greatly from that of November 2nd, yet the population diversity, as well as total population, on the earlier date was quite high. Variation in response of different insects to the environmental factors considered affects the correlation at certain points. In the serotine sector of each year such a correlation failure occurs, the vapor pressure deficit-light factor being low but the population high. This appears to be due to the sudden influx of families responding positively to increased humidity (Fungivoridae, Psychodidae, Trichoceridae, Tendipedidae, etc.), even though the occurrence of these same insects later corresponds to the environmental curve in the usual way. It also may be assumed that some environmental factors vary in their effect on variety of insect fauna, depending upon the relationship of those factors to several other undetermined factors, while others (e.g. temperature), are undoubtedly cumulative in effect. Additional factors that are known to affect fluctuations of populations but which were not directly considered, are ultraviolet radiation (Shelford 1951) and length of day (Allee *et al.* 1949).

Thus for this investigation the biotic aspects were first determined roughly by noting the dates when the curve of population and the curve of vapor pressure deficits and light (Fig. 10) indicated extreme fluctuation. By referring to the columnar portion of the graph, it was possible to determine whether this fluctuation was due to addition or loss of groups of animals or both. Field notes were then consulted to determine whether the general picture of faunal population, vegetational development and environmental conditions indicated a change at this point. The hygrothermograph records were found to be a valuable index for setting dates of meteorological departure from a normal seasonal pattern. Each season appeared to have a unique relationship between temperature and humidity as illustrated for typical periods (Figs. 11 & 12). The pattern for each season was easily recognizable, in spite of variations and temporary departures from the normal. When this pattern changed distinctly, it was usually possible to discover a correlated alteration in the composition of the population. In the fall of the year more difficulty is encountered in establishing definite dates for the terminations of seasons than at any other periods.

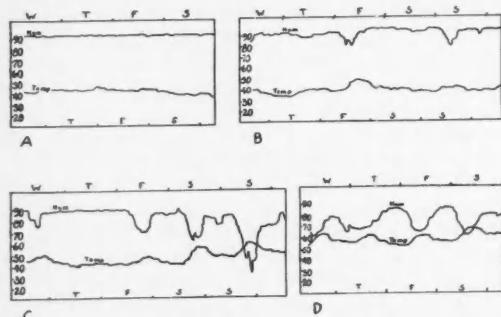


FIG. 11. Sample hygrothermograph records showing typical seasonal patterns. A. Record for the period from Dec. 7, 1936 to Dec. 10, 1936, showing the uniformly high humidity and moderately low temperature, with extremely slight diel fluctuation, characteristic of the hiemine sector. B. Record for the period from March 10, 1936 to March 15, 1936, showing the high humidity and moderately low temperature, with slight diel fluctuation, characteristic of the emergine sector. C. Record for the period from May 4, 1936 to May 9, 1936 illustrating the increasing daily fluctuation in humidity and temperature, with lowered humidity and increased temperature, characteristic of the transition from the preverine to the vernine sector of the vernal aspect. D. Record for the period from July 15, 1936 to July 19, 1936, indicating the characteristic diel alternation in the aestival aspect, from high temperature and low humidity to low temperature and high humidity.

The faunal fluctuations at that time of the year are much smaller and representatives of the population drop out at various points. Hardier types of animals are not taken during unfavorable periods and reappear later when the weather moderates. Meteorological factors in the autumn are subject to wide fluctuations and in some years of this study the seasons passed almost imperceptibly into the succeeding stage of aspect. Hence, it is felt that some of the attempts to date the termini definitely may be rather arbitrary, especially in view of the fact that collections and observations were made a week or more apart.

The seasons tentatively determined by these data were then checked against graphs of temperature, humidity and precipitation, an attempt being made to determine whether a unity or continuity of character was shown by these separate factors, and, if not, whether adjustments in seasonal limits might be made which would improve the seasonal picture.

BIOTIC ASPECTS IN THE OREGON COAST RANGE FOREST

As a result of the above-mentioned considerations of environmental and biotic data, it has been possible to piece together a panorama of the seasonal changes by means of a combination of environmental, vegetational and faunal analyses. These seasonal changes include both major and minor biotic divisions. The four aspects or major biotic seasons are termed the hiemal, vernal, aestival and autumnal aspects. Nine biotic subdivisions or seasonal societies of the four

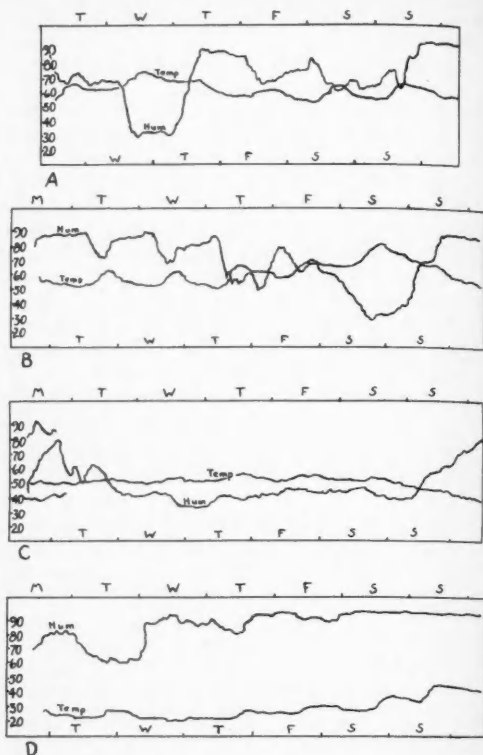


FIG. 12. Sample hygrothermograph records showing typical seasonal patterns. A. Record for the period from Aug. 27, 1936 to Sept. 2, 1936, showing a short period of very low humidity on Aug. 28, such as is often characteristic of the change from the aestival to the autumnal aspect (serotinine sector). B. Record for the period from Aug. 28, 1934 to Sept. 4, 1934, illustrating the unstable moisture conditions, with fluctuations extending over several days, which are characteristic of the autumnine sector, i.e., a period of low humidity extending over several days, with a return to humid conditions of similar duration. C. Record for the period from Nov. 21, 1936 to Nov. 29, 1936, showing the type of fluctuation characteristic of the autumnine sector, i.e. a period of low humidity extending over several days, with a return to humid conditions of similar duration. D. Record for the period from Feb. 15, 1936 to Feb. 22, 1936, showing the characteristic hibernine pattern, i.e., a cold, dry spell, with return to high humidity and higher temperature.

major aspects are found. These subdivisions are termed *sectors*, the names of which are given the suffix *-ine* in preference to the *-al* suffix which heretofore has been used to designate both major and minor biotic seasons. The winter or hiemal aspect consists of three sectors, hiemine, hibernine and emergine; the spring or vernal aspect includes the preverine and vernine sectors; the summer or aestival aspect shows a division into early (cisaestine) and late (aestine) sectors; while the fall or autumnal aspect includes the serotinine and autumnine sectors.

TABLE 1. Dates of seasonal limits.

Year	1st	2nd	3rd	4th	5th	6th
HIEMAL ASPECT						
Hiemine Sector						
Start	Oct. 30, '32	Nov. 1, '33	Nov. 17, '34	Oct. 26, '35	Nov. 28, '36	Nov. 8, '37
End		Dec. 15, '33	Dec. 28, '34	Dec. 15, '35	Dec. 26, '36	Dec. 19, '37
Hibernine Sector						
Start		Dec. 15, '33	Dec. 28, '34	Dec. 15, '35	Dec. 26, '36	Dec. 19, '37
End	Feb. 25, '33	Jan. 25, '34	Jan. 24, '35	Mar. 1, '36	Feb. 20, '37	Jan. 9, '38
Emerginine Sector						
Start	Feb. 25, '33	Jan. 25, '34	Jan. 24, '35	Mar. 1, '36	Feb. 20, '37	Studies
End	Apr. 1, '33	Mar. 10, '34	Apr. 9, '35	Apr. 7, '36	Mar. 30, '37	Terminated
VERNAL ASPECT						
Prevernine Sector						
Start	Apr. 1, '33	Mar. 10, '34	Apr. 9, '35	Apr. 7, '36	Mar. 30, '37	
End	May 20, '33	Apr. 10, '34	Apr. 23, '35	May 5, '36	May 1, '37	
Vernine Sector						
Start	May 20, '33	Apr. 10, '34	Apr. 23, '35	May 5, '36	May 1, '37	
End	June 12, '33	May 27, '34	June 5, '35	May 25, '36	June 24, '37	
AESTIVAL ASPECT						
Cissastine Sector						
Start	June 12, '33	May 27, '34	June 5, '35	May 25, '36	June 24, '37	
End	July 15, '33	July 1, '34	July 9, '35	July 8, '36	Aug. 4, '37	
Aestine Sector						
Start	July 15, '33	July 1, '34	July 9, '35	July 8, '36	Aug. 4, '37	
End	Aug. 13, '33	Aug. 22, '34	Aug. 17, '35	Aug. 28, '36	Aug. 30, '37	
AUTUMNAL ASPECT						
Serotinine Sector						
Start	Aug. 13, '33	Aug. 22, '34	Aug. 17, '35	Aug. 28, '36	Aug. 30, '37	
End	Sept. 15, '33	Oct. 7, '34	Oct. 5, '35	Oct. 19, '36	Oct. 13, '37	
Autumnine Sector						
Start	Sept. 15, '33	Oct. 7, '34	Oct. 5, '35	Oct. 19, '36	Oct. 13, '37	
End	Nov. 1, '33	Nov. 17, '34	Oct. 26, '35	Nov. 28, '36	Nov. 8, '37	

Dates for the seasonal limits of these aspects and seasons are given in Table 1. The biotic aspects generally precede the calendar seasons and are affected by climatic conditions which shorten or lengthen their duration. The opening dates of the vernal aspect in this location fluctuated about the date of the spring equinox while the aestival aspect started before the summer solstice in every year but 1937. Acceleration of biotic seasons is also shown by the opening of the serotinine sector of the autumnal aspect approximately one month before the autumnal equinox and by the beginning of the early sector of the hiemal aspect which started, on the average, a month and a half ahead of the winter solstice.

Hiemal Aspect

The winter, or hiemal aspect as a whole, is the period of unfavorable physical factors of the environment with a correspondingly restricted biota. Though moderate and with transitional phases at either end, the winters in this community are rather extensive, being over four months in length. The hiemal aspect usually begins in late October or mid-November and ends around the first of April. The invertebrate population consists chiefly of a characteristic group of

Trichoceridae, Fungivoridae, Psychodidae and spiders all of which have been elements of the autumnal fauna. It is low both in number of individuals and diversity of species during the hiemine sector and becomes very restricted in the hibernine sector of this aspect, but awakens to greater activity in the late or emerginine sector when it is considerably augmented by a group of animals destined to become a part of the fauna of the vernal aspect. Table 2 and Figure 13 show that only 25 species of insects are characteristic of the hiemal aspect. Of these species none begins its activity in the hiemine sector, one begins in the hibernine sector and twelve in the emerginine, the remainder having been a part of the autumnal fauna. None of these is restricted to the hiemine nor hibernine sector and only three (12%) are restricted to the emerginine sector. Diptera represent 44% and Coleoptera 20% of the hiemal fauna. The hiemine sector has a more varied population than the hibernine, which is the low point for the year, while the emerginine has the greatest population of the winter. Temperatures lie almost entirely below the average annual mean of 50° F (Fig. 14), and humidity is high (75-90%). Vapor pressure deficits therefore are low, the weekly maxima averaging less than .100

TABLE 2. Seasonal distribution of insects characteristic of the hiemal aspect (winter). E, emergine sector; PV, prevernine sector; SV, vernine sector; CA, cisaestine sector; SA, aestine sector; S, serotinine sector; A, autumnine; H, hiemine sector; Hi, hibernine sector; X, characteristic of a given aspect; --, present but not in significant numbers. The seasonal distribution of each insect considered is tabulated throughout the year but is not repeated on any other chart unless characteristic of that season, i.e., was collected more than once during a given season for at least three of the five years studied.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Collembola									
Entomobryidae: <i>Tomocerus flavescens</i> Tullb.	X	X	X	X	--	X	X	X	
Sminthuridae: <i>Plenothrix</i> sp.	X	X	X	X	--	X	X	X	
Hemiptera									
Aleyrodidae: gen. et sp. indet.	X	X	X			X	X	X	--
Coccoidea: indet.	X						X	X	X
Hemiptera									
Pentatomidae: <i>Elasmothus cruciatus</i> Say	X								X
Lygaeidae: <i>Ichnorhynchus resedae</i> Pans.	X								
<i>Gastrolea pacifica</i> Prov.	X								
Coleoptera									
Staphylinidae: <i>Anthobium subcostatum</i> Maekl.		X					X	X	
<i>A. pictum</i> Fauvel		X					X	X	
Cerambycidae: <i>Plectrura spinicauda</i> Mann.		X	X	X	X	X	X	X	
Cureulionidae: <i>Nemocetes incomptus</i> Horn.		X	X	X	X	X	X	--	
<i>Sciophilus obscurus</i> Horn.		X	X	X	X	X	X	--	
Diptera									
Trichoceridae: <i>Trichocera pallens</i> Alex.	X						X	X	X
Psychodidae: <i>Psychodes</i> sp.	X	X	X			X	X	X	X
Culicidae: <i>Culiseta incidens</i> (Thoma.)	X	X	X	X	X	X	X		
Fungivoridae: <i>Erechia</i> sp.	X	X					X	X	X
<i>Pungitara</i> sp. 1.	X	X				X	X	X	
<i>Diadocides borealis</i> Meig.	X	X							
<i>D. ferruginea</i> Meig.	X	X							
<i>Mycomya</i> sp.	X	X							
<i>Monoclonia</i> sp.	X								
Phoridae: <i>Triphleba</i> sp.	X						X	X	X
Anthomyiidae: <i>Pegomya</i> sp.	X	X					X		
Lepidoptera									
Gracilariidae: <i>Cameraria gaultheriella</i> (Wishm.) larvae	X	X					X	X	X
Hymenoptera									
Belytidae: <i>Xenotoma</i> sp.	X	X	X		X	X	X		
Total	20	18	9	6	7	10	18	15	8

mm Hg. The light intensity is also very low, averaging less than 25% of full sunlight. Precipitation is high, averaging 2-3 in. per week.

Hiemine Sector: This subseason or sector of the winter season may be characterized as the portal for entrance into the dormant phase of winter. It generally starts about the first week in November, the extremes being October 26, 1935 and November 23, 1936. The average duration is approximately one month, terminating in December. The hiemine sector of winter has very little botanical evidence of a positive nature to distinguish it. Leaves have disappeared from all deciduous shrubs and trees leaving only the evergreen foliage of salal, Oregon grape,

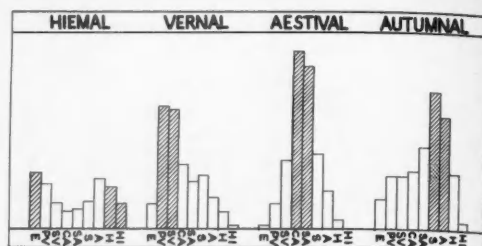


FIG. 13. Totals of common species of insects characteristic of each aspect (shaded columns) and their seasonal distribution throughout the remainder of the year (unshaded columns). Compiled from tables of seasonal occurrence of insects by D. McKey-Fender.

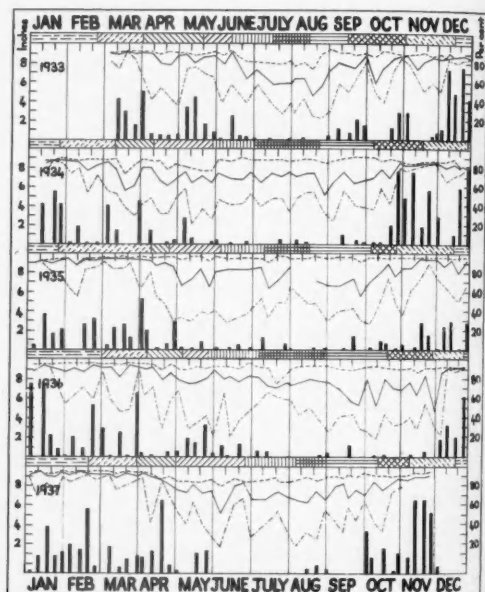


FIG. 14. Weekly maximum, mean and minimum relative humidity and total weekly precipitation. Broken (short dash) line—maximum humidity; dot-dash line—minimum humidity; solid line—mean humidity. (This figure was obtained by averaging readings arbitrarily selected at 12-hour intervals for the week preceding each collecting date). Scale—1 unit equals 2% of relative humidity. Columns show weekly precipitation as measured by the rain gauge located beneath an opening in the canopy at Instrument Location A. Scale—5 units equal 1 inch of precipitation. Seasonal limits indicated as in Figure 10.

sword fern, deer fern and conifers, bringing out the basic evergreen character of the vegetation of this community. Mosses and lichens brighten up and some mosses produce capsules at this time.

A sharp drop in variety of insects is associated with the end of the autumnine and beginning of the hiemine sectors. The hiemal aspect begins when all hymenoptera, most diptera and most coleoptera disappear, leaving only a few families of insects which are ac-

tive consistently. Fungivoridae, Psychodidae and Trichoceridae are particularly characteristic. Aleyrodidae occur quite generally but are not active and decline in numbers as the sector wears on. Collembola (*Tomocerus flavescens* Tullberg and *Ptenothrix* spp.) characterize the hiemine sector by appearing in considerable numbers on the shrubs and hemlocks, even having been collected in the top of the large hemlock designated Location G (Figs. 4 & 5). Except for the cerambycid beetle *Plectrura spinicauda* Mann. and two weevils (*Nemocetes incomptus* Horn and *Sciopithes obscurus* Horn) the insects are all very small. Work of the salal leaf miner larvae (*Cameraria gaultheriella* (Wlsh.)) is noticeable at this time (Table 2). Adult spiders are present but are only active on warm days. They remain under leaves in a semidormant condition most of the time. Slugs still occur occasionally on the forest floor. Amphibia are sluggish and not frequently encountered.

This is the only sector in which no new species of insects are added to the population, which is low in number of individuals and variety of species, the graphed population line (Fig. 10) descending toward its winter low. Thirteen species of insects are recognized as common in this sector, all of which remain through to its end (Table 2). *Hylemya alcatheae* Walk., *Vespula vulgaris* L., several beetles and several of the Ichneumonidae characteristic of the autumnal aspect terminated their activity early in the hiemal aspect in some years, but the autumnal fauna in general disappeared at the beginning of the hiemal aspect.

Flocks of red-breasted nuthatches (*Sitta canadensis* L.), Sitka red crossbills (*Loxia curvirostra sitkensis* L.), Pacific varied thrushes (*Ixoreus naevus* (Gmelin)), chickadees (*Parus rufescens* (Townsend)) and *P. atricapillus occidentalis* Baird), kinglets (*Regulus satrapa olivaceus* Baird and *R. calendula grinnelli* (Palmer)) and California creepers (*Certhia familiaris occidentalis* (Ridgway)) are common at this time. Western pileated woodpeckers (*Dryocopus pileatus picinus* Bangs), Oregon gray jays (*Perisoreus canadensis obscurus* Ridgway) and juncos (*Junco hyemalis oregonus* Townsend and *Junco hyemalis shufeldtii* Coale) which are present during the hiemine sector, migrate to lower levels toward its close, appearing this high on the mountain only in warm periods of the succeeding (hibernine) sector. The population of permanent resident birds becomes noticeably decreased at the close of this sector.

From a meteorological standpoint the opening of the hiemal aspect seems to correlate well with the descent of weekly minimum temperatures to the vicinity of 40° F. Sometimes this drop immediately precedes the opening of the aspect. Within the hiemine sector the weekly minimum may temporarily rise above this level. On the whole, minimum temperatures remain well below 40° F during the hiemine sector. The maximum temperature is generally quite consistent, the seasonal means of maximum temperature ranging near 50° F, whereas the mean minimum shows much greater variation. The maximum temperatures are

so stable that one might say a lid or ceiling has been placed on the temperature allowing very little fluctuation at the upper limits but placing less restriction on the lower levels. The mean temperatures for the sector varied very little from year to year averaging 43.5° F. The hiemine sector appears to terminate when the temperature range becomes practically restricted to a zone between 50° and 30° F (Fig. 15). Precipitation varies widely, from a weekly average of 0.77 in. in 1933 to a maximum weekly average of over 5.41 in. in 1937 (Fig. 14). The humidity in general is high, the 5-year average of the seasonal mean being 86% (Figs. 11a, 14). Wind direction is from all points of the compass, but predominantly from the southwest with north and northeast winds occurring frequently. The wind velocity is in general moderate, although southwesterly gales lasting a few days may occur. The weather is predominantly cloudy during this season, interspersed with clear periods of a few days' extent. Vapor pressure deficit descends during this sector to the low level of the winter and in most years remains relatively stable throughout the season (Table 3).

Hibernine Sector: This is the comparatively severe portion of the winter and is designated as the period of deepest dormancy from a biotic standpoint. Heretofore authors have used the terms hibernal and hiemal more or less synonymously, but, in view of the need for a refinement of aspectional terminology disclosed by this author's studies, it seems best to allocate the term hiemine to the sector of the winter season in which animals are going into hibernation and to use hibernine for the sub-season or sector in which hibernation is at its maximum. Because of the moderate winters in this region a small group of invertebrate species may be active even in the hibernine sector of the hiemal aspect. In winters of extreme cold and during the coldest weather of mild winters, all invertebrates above ground are in a dormant state.

Usually this sector begins in the middle of December and ends in mid-February. It is a rather long sub-season, averaging seven weeks. The shortest hibernine sector was in 1934 when it lasted only four weeks.

Higher plants are all dormant and there is no particular evidence of any activity in the lower types.

The hibernine sector is primarily the dormant season of the invertebrate population above ground at this location. With the beginning of this sector, 8 of the hiemine species drop out altogether (Table 2), while the only invertebrate typically added to the population during this period is a pentatomid bug (*Elasmotherethus cruciatus* Say) which was obtained from hemlock boughs even when they were loaded with snow. In common with the other characteristic hibernine species, this bug extends into the emergine sector.

There are no animals entirely confined to this sector. Those discussed as being especially characteristic of the hiemine sector are also characteristic of the hibernine sector. The difference lies in the fact that in the hibernine sector these insects are barely main-

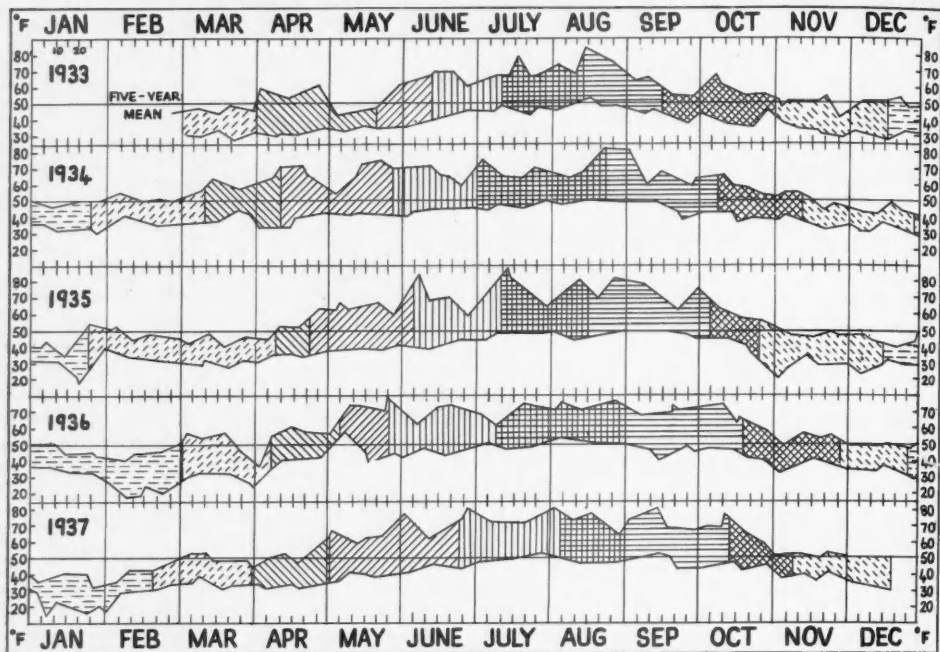


FIG. 15. Weekly maximum and minimum temperatures, from Weather Bureau maximum and minimum thermometers in the shrub level. Upper line—maximum; lower line—minimum. Shading between the two lines indicates the seasonal limits as shown by the key accompanying Figure 10. A five-year mean, which is approximately the mean annual temperature for each of the five years, is indicated by a light solid line at the 50° F level.

taining an existence and activity is at a low ebb. The Fungivoridae, Trichoceridae, Aleyrodidae and Psychodidae so characteristic of the hiemine sector, are usually found in apparent hibernation during the hibernine sector quietly hanging beneath salal leaves and only flying rather sluggishly on rare occasions when the temperature permits limited activity. During this sector several types of invertebrates are absent which are present in every other season; these include collembola and mollusca. Only eight species of insects are at all common during this sector, the active population above ground on any one collecting day consisting of only two or three families of insects. Amphibia, chipmunks and bears are known to hibernate during this period. Tracks of rabbits, the snow-shoe hare (*Lepus americanus washingtonii* Baird) and the brush rabbit (*Silvilagus bachmani ubericolor* (Miller)), bobcat (*Lynx rufus fasciatus* Raf.), cougar (*Felis concolor oregonensis* Raf.), civet cat (*Spilogale phenax latifrons* Merriam) and white-footed deer mice (*Peromyscus maniculatus rubidus* Osgood) and other mice were noted during snowy periods. Tracks of the Columbian black-tailed deer (*Odocoileus hemionus columbianus* (Rich.)) were seen, but not so frequently as later.

Environmentally, this sector of winter is characterized by cold, rainy weather and occasional heavy snows. Predominantly cloudy weather may be inter-

spersed with brief spells of clear, frosty days (Fig. 12d). The sector seems to be initiated by a drop in temperature immediately preceding or following the opening date. The range of temperatures may be very wide, a variation of more than 25° within the week being not uncommon. The lowest temperatures of the year are recorded during this season, maxima and minima both being low. Minimum temperatures may drop considerably below freezing, but usually hover around 30° F. The maximum temperatures generally range between 40 and 50° F. In the years under consideration, the close of the season was marked by a definite rise in temperatures, both maximum and minimum. At either end of the sector, the trend of temperature appears to be more significant than the actual temperatures recorded (Fig. 15). The average precipitation is higher than during the hiemine sector and does not show so much variation. The seasonal average varies from 1.35 to 4.00 in./wk, making it the season of heaviest precipitation, much of which in most years is in the form of snow. Humidity is high, averaging 92%. Low humidity may occur during clear weather (Fig. 12d). Wind velocity shows extreme variation from very light breezes to gales. The predominating wind comes from the southwest. East winds are more frequent than in the hiemine sector, and are associated with low temperatures. The low light intensity averages much the same as in

TABLE 3.* Seasonal averages of meteorological data for the hiemal aspect.
H—hiemine sector; Hi—hibernine sector; E—emerginine sector; T—entire hiemal aspect.

	First Winter	Second Winter				Third Winter				Fourth Winter				Fifth Winter				Sixth Winter				Averages			
	E '33	H'33	Hi'33	E'34	T	H'34	Hi'34	E'35	T	H'35	Hi'35	E'36	T	H'36	Hi'36	E'37	T	H'37	H	E	T	H	E	T	
Temperature																									
Maximum	46.6	51.8	50.0	51.3	50.9	47.4	41.0	48.0	46.0	50.0	45.4	49.4	47.7	51.0	39.1	47.8	44.7	51.4	50.3	43.6	48.6	47.3			
Minimum	31.6	34.7	33.6	37.1	35.1	36.0	28.5	31.0	32.0	29.2	32.6	29.2	30.9	34.2	21.8	33.7	28.0	36.4	34.2	27.6	32.5	31.5			
Mean	39.1	43.1	42.3	44.2	43.0	42.7	34.7	39.5	39.5	43.9	36.9	39.2	39.4	42.9	30.5	40.5	36.6	43.9	43.5	35.8	40.5	39.5			
Range	15.0	16.8	16.3	14.1	15.1	11.4	12.0	17.0	12.8	20.8	17.5	20.0	19.1	16.7	17.1	14.5	15.6	15.4	16.7	15.8	16.1	15.3			
Relative Humidity																									
Maximum	92.2	89.4	90.0	90.7	87.5	90.5	94.9	91.8	96.0	95.2	95.6	95.6	97.7	94.8	95.5	94.5	95.0	92.6	92.4	94.0	93.1			
Minimum	71.4	85.2	72.0	73.2	78.0	86.5	78.9	80.1	66.0	76.5	66.0	70.0	60.8	85.5	85.0	79.4	90.8	73.3	83.4	75.4	75.6			
Mean	87.7	89.4	82.0	87.7	85.2	85.5	90.9	88.7	88.7	91.8	90.1	90.2	80.6	92.3	93.0	89.7	94.3	86.6	89.7	90.5	86.5			
Range	20.5	4.2	18.0	14.6	9.0	4.0	16.1	13.7	30.5	17.5	29.6	25.1	32.2	9.2	10.6	15.0	4.1	19.1	8.7	18.5	17.8			
Precipitation	2.87	1.60	4.77	1.63	2.61	2.70	1.35	2.05	2.56	2.16	2.92	2.03	2.18	1.79	2.58	2.28	1.93	5.41	2.73	2.90	2.17	2.32			
Light	11.8	30.0	22.5	25.0	25.0	21.0	30.0	28.9	27.4	10.0	21.8	26.6	19.5	21.2	25.7	28.0	21.5	20.0	20.4	25.0	24.0	24.2			
Evaporation	1.27	1.04	0.75	1.48	2.80	2.89	0.48	1.34			
Vapor Pressure Deficit																									
Maximum099	.046	.072	.063	.060	.047	.053	.059	.074	.048	.097	.068	.077	.022	.049	.040077	.040	.067	.057			
Mean036	.026	.035	.032	.041	.023	.021	.026	.029	.019	.024	.025	.058	.013	.018	.025	.039	.040	.020	.024	.029			

*Sources of meteorological data are as follows: Temperature (°F), from Weather Bureau maximum and minimum thermometers; Figures given are means of maximum, minimum, median and range as read each week. Relative humidity (%), from hygrothermograph: Figures are means of weekly readings of maximum, minimum and range, mean from daily median. Precipitation (inches), from rain gauge under opening in canopy: Figures given are means of weekly totals. Light: Figures given are means of % of full sunlight on the day observations were made. Evaporation, from Livingston cup atmometer: Figures given are means of cubic centimeters water evaporated daily. Vapor pressure deficit (inches Hg.), from hygrothermograph records: Figures given are means of maximum, minimum and median weekly vapor pressure deficit readings. Wind velocity, from cup anemometer readings: Figures given are means of miles recorded per day. All readings were at the shrub level.

the hiemine sector, while vapor pressure deficit, though low, varies more widely. This variation of the vapor pressure deficit is apparently correlated with the periods of clear, cold weather characteristic of this season (Table 3).

Emerginine Sector: At this location and elevation there is a definite stirring of activity and emergence from dormancy on the part of the animal life before blossoms appear on any plants. The term *vernal* was introduced by botanists to indicate the flowering stage of spring flora. *Prevernal* was added to separate the blooming period of the very earliest plants from the more typical spring flowers. Thus the terms *vernal* and *prevernal* have come to have a definite association with blossoming of certain plants. It is proposed therefore that the term *emerginine* be adopted where it is necessary to designate a sub-season or sector of winter in which hibernation is definitely in the process of breaking up, the hiemine fauna have renewed their activities and some animals have become active in anticipation of their role as typical *prevernal* species. This proposal would be in recognition of the fact that flowers are not the first indicators of the approach of spring.

This sector is typically 5 weeks in length, although in 1935 it lasted 10 weeks, establishing the earliest opening date, January 24, and the latest closing date, April 9 (Table 1, Fig. 16). The period covered by the emerginine sector is extremely variable, as are the meteorological and faunal characteristics of this season (Fig. 10).

An emerginine sector is indicated vegetationally by a greener tinge in the bark of deciduous trees, by

swelling buds and sprouting herbs and shrubs. No flowers are yet in evidence.

The initiation of the emerginine sector is not definitely characterized by the activity of any one species of invertebrate. Several species were used in attempting to fix approximate opening dates but all failed in one or more years because of insufficient specimens to form a complete record. This sector proved a difficult one in which to obtain satisfactory data. The weather at this time of the year is so variable that organisms could be active between collecting dates and yet unavailable on the date of collection because of low temperatures, high humidity, snow or rain. This, coupled with the paucity of insect life even under the best of conditions, caused the records to be incomplete. The rain barrel mosquito (*Culiseta incidens* (Thoms.)) was the best indicator except in 1936, when it was not noted until the close of the aspect. *Tendipedidae* and a *lygaeid* bug (*Ischnorrhynchus resedae* Pans.) initiated the sector very consistently except in 1935. In that year they occurred before the beginning of the emerginine sector which was definitely established by the environmental data and general collection records. An anthomyid fly (*Pegomya* sp.) was collected at the beginning of the sector in 1936 and 1937. To obtain an opening date for the emerginine sector, it was necessary therefore to strike a mean point between the first occurrence of several of these forms, taking the environmental records also into account. Although this sub-season is a definite unit, more careful collecting is needed to establish dependable faunal indicators for its initiation. Sporadic evidences of activity of moles (*Scapanus o. ora-*

INVESTIGATOR	COMMUNITY	LOCATION	N. LAT.	DATE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Brown 1931	Oak-hickory	Ohio	35°	1927												
Shufeldt 1926	Prunus	Ohio	35°	1933												
Shufeldt 1926	Prunus	Ohio	35°	1934												
Shufeldt 1926	Prunus	Ohio	35°	1935												
Adams 1934	Elm-maple	Tenn.	34°	1934												
Smith 1928	Sand Shrimp	Ill.	40°	1925												
Davidson 1930	Maple-redstart	Ill.	40°	1926												
Wheeler 1924	Elm-maple	Ill.	40°	1927												
Carson 1935	Prunus, forest	Cent. Ill.	40°	1935												
Reed + Clements 1900	Prunus	Nebbraska	40°	1900												
Mason + Fitzgerald 1924	Prunus	Nebbraska	40°	1924												
Fichter 1932	Prunus	Nebbraska	40°	1932												
Truman 1915	Elm-maple	Ill.	40°	1915												
Shufeldt 1929	Prunus	Ill.	40°	1929												
Williams 1924	Beach maple	Ohio	45°	1924												
Macnab 1914	Forest of	Oregon	45°	1914												
				1915												
				1916												
				1917												

FIG. 16. Seasonal limits. Aspectional studies of various authors in the United States brought together, making possible a comparison of the period covered by each season in each year for the several communities and geographic locations involved, as well as a comparison of the terminology used in each case. Geographic location, biotic community, latitude and dates of observation are specified for each. Sectors of this author are keyed as in Figure 10. In the case of authors having an undivided prevernal-vernal aspect only one of the vernal sector symbols is shown; the symbol for the hibernial sector of this author (diagonal broken lines) is used for the winter aspect of other authors, whether termed hibernial or hibernial; the symbol for the early sector of the aestival aspect (vertical lines) is used for the aestival aspect of others.

True), shrews (*Sorex t. townsendii* Baird), mice and an occasional chipmunk (*Eutamias t. townsendii* Bachman) were encountered throughout this sector. Pacific varied thrushes were present singly or in pairs rather than in flocks. Gray and Stellar jays, pileated woodpeckers and juncos returned to the area.

The Trichoceridae which are found in the hibernine sector are characteristic and abundant here. Several species of Fungivoridae are present. A group of hemiptera are especially characteristic and frequently collected, although never abundant. These animals hibernate as adults in cracks of bark and other sheltered places during the hiemine and hibernine sectors but are collected very infrequently in these sectors. Not more than twelve and usually only five or six different families of insects were active in the shrub level on any one collecting day during the emerginine sector. The total number of individuals active in this sector is also low. A few insects characteristic of the vernal aspect begin their activity within the emerginine sector. Among these are occasional muscoid flies, Geometridae, a few Staphylinidae and occasional Ichneumonidae.

The close of the emerginine sector is marked by the absence of the hemiptera as well as Trichoceridae and

by the appearance of *Calliphora vomitoria* L., Lycidae, a number of Staphylinidae and the geometrid moth *Mesoleuca gratulata* Walk. (Table 2.)

Generally the emerginine sector is cloudy and rainy with snow falling occasionally at this elevation. The sector starts environmentally when the maximum temperatures first rise above the annual mean of 50° F in the spring regardless of whether they drop below this point later in the season. The minimum temperatures do not seem to be significant, as they may drop well below freezing during the sector without permanently affecting the insect population. The close of the season is marked by a rise in maximum temperatures which often reach at least 60° F. The weekly minimum temperatures also rise permanently above 30° F around which they previously oscillated, although their rise tends to lag behind the rise in maximum temperatures (Fig. 15). The weekly average precipitation for the sector in all years dropped below 2.5 in. (Table 3). Rains are not as heavy as in the hibernine sector. Winds are light to moderate with southwest winds predominating. Northeast winds occur frequently. Humidity is high, having averaged 90.5% during this sector for the duration of the records. There is an increased range in relative humidity during this sector. Average light intensity is low, being practically the same in the emerginine as in the hibernine sector. There is a pronounced though slight rise in vapor pressure deficit at the beginning of this sector, which is maintained with little fluctuation throughout the emerginine sector. A still more pronounced rise in vapor pressure deficit at the close of the emerginine initiates the vernal aspect.

VERNAL ASPECT

In line with the plant ecologists' policy of confining the term prevernal to the dates of earliest spring flowers and vernal to the later more typical spring flowers, the flowering plants of this community show quite clearly two distinct vernal sectors. Division of the vernal aspect into two subseasons or sectors is also shown by an influx of new invertebrate species between the two subdivisions, materially altering the composition of the population of the later sector. The meteorological factors also show a break in the environmental transition, from wet to dry, and cold to warm weather, which accentuates the division into early and late sectors. The faunal records as a whole bind the two vernal sectors rather closely, however, so that the picture obtained is that of a single season rather than two seasons. It seems best, therefore, to designate the prevernal and vernal aspects of other authors as early and late subseasons rather than seasons. This being the case, the terms *prevernal* and *vernal* are not as desirable as *prevernal* and *vernal* sectors which are two parts of a unit called the spring or vernal aspect.

The vernal aspect is characterized as the season when unfolding buds add a fresh tinge of green to plants of the shrub layer and when the growth of

herbs covers the forest floor with a carpet of green leaves and flowers.

The vernal aspect is generally quite extensive, averaging about eight weeks in extent. The opening date is generally early in April (Table 1). The earliest termination was May 25, 1936 and the latest June 24, 1937. Both the early and late sectors exhibited considerable variability in duration from a minimum of two weeks for both subseasons in 1935 to around 7 weeks for the prevernal sector in 1933 and 7 weeks for the vernine sector in 1934 (Fig. 16).

The occurrence of numerous pollenophagous insects is correlated with the presence of blossoming herbs. Coleoptera characterize the vernal aspect by their abundance, at least 40 species having been collected more than once in this season during the 5-yr period, 34.3% of common vernal insects belonging to this order. Diptera also reach a peak of abundance and variety during this period, 53 species having been collected, which indicates the dipterous nature of this community. Only 19 species occurred commonly enough to be included on the charts of common insects (36.2% of the total). Crane flies of the family Tipulidae replace the smaller Trichoceridae characteristic of the winter aspect. Tendipedidae, Simuliidae and Psychodidae are abundant. Muscoid flies are very common while Syrphidae and Bibionidae are only slightly less abundant. Geometridae emerge in numbers. Hymenoptera, which represent 14.5% of the vernal species, show a greater variety than at any other season except the autumnine (late autumn), when they are also abundant, but then chiefly represented by the smaller parasitic species (Table 4). Of the 55 species of insects occurring commonly in the vernal aspect, most (80%) begin their activities during the aspect, the remaining species having been part of the hiemal fauna. Nearly half (43.6%) of the species are restricted to the vernal aspect, 16.3% being restricted to the prevernal sector and only 9% to the vernine. Over half of the vernal species (54.5%) occur in both sectors of the aspect, 23.4% being present in the prevernal sector but not in the vernine and 21.8% in the vernine but not the prevernal sector. In general, the vernal aspect population drops suddenly at the beginning of the eisaestine sector and then dwindles away gradually through the remainder of the year. The greater height of the serotonin column over the aestine (Fig. 13, vernal) is due to a resurgence of insects responding positively to increased moisture.

The vernal aspect is a season of transition from wet to dry and cold to warm environment (Table 5). The factors of moisture and temperature are, in general, intermediate between winter and summer but are progressing with fluctuations toward the conditions typical of summer. The minimum temperature averages well above the freezing point, although occasional frosts do occur. The maximum for the vernal aspect averages around 60° F and the seasonal mean 40° F. Wind direction for the vernal aspect is characterized

TABLE 4. Insects characteristic of the vernal aspect (spring). Explanation as in Table 2.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Collembola									
Entomobryidae: <i>Tomocerus flavescens</i> Tullb.	X	X	X	X	--	X	X	X	
Smithuridae: <i>Plenothrix</i> sp.	X	X	X	X	--	X	X	X	
Homoptera									
Aleyrodidae: gen. et sp. indet.	X	X	X			X	X	X	--
Cicadellidae: <i>Errhonus oregonensis</i> Baker		X	X						
Coleoptera									
Carabidae: <i>Scaphinotus angusticollis nigripennis</i> Roesch.			X	X		X	X		
Staphylinidae: <i>Anthobium subcostatum</i> Mackl.		X					X	X	
<i>A. pictum</i> Fauvel		X					X	X	
<i>Pelocoma testaceum</i> Mann.		X							
Lycidae: <i>Dictyopterus simplicipes</i> (Mann.)		X							
Cantharidae: <i>Podabrus piniphilus</i> (Esch.)			X	X					
Elaterridae: <i>Ctenicera mendax</i> Lec.			X						
Byrrhidae: <i>Listemus acuminatus</i> (Mann.)		X							
Nitidulidae: <i>Epurea</i> sp.		X	X						
Melandryidae: <i>Prothalia holmbergi</i> (Mann.)		X	X	X					
Cerambycidae: <i>Eiodinus vancouveri</i> (Csy.)		X	X						
Chrysomelidae: <i>Timarcha intricata</i> Hald. larvae		X	X						
Cureulionidae: <i>Nemocastes incomplus</i> Horn.		X	X	X	X	X	X	X	
<i>Stremneus tuberosus</i> Boh.		X	X	X	X	X			
Scolytidae: <i>Pseudohylesinus grandis</i> Sw.		X	X	X	X				
<i>P. sericeus</i> (Mann.)		X	X	X	X				
<i>Gnathotrichus sulcatus</i> (Lec.)			X	X	X	X			
<i>Dendroctonus pseudotsugae</i> Hopk.		X	X						
Diptera									
Tipulidae: <i>Limonia infusata</i> (Doane)		X	X						
Simuliidae: <i>Prosimulium</i> sp.		X	X	X					
<i>Prosimulium fulvum</i> Coq.			X	X					
Psychodidae: <i>Psychodes</i> sp.	X	X	X			X	X	X	X
Culicidae: <i>Culiseta incidens</i> (Thoma.)	X	X	X	X	X	X	X		
Fungivoridae: <i>Diadocidea borealis</i> Meig.	X	X							
<i>D. ferruginosa</i> Meig.	X	X							
<i>Fungivora</i> sp. 1.	X	X				X	X	X	
<i>Fungivora</i> sp. 2.	X	X							
<i>Boletina</i> sp.	X	X							
Bibionidae: <i>Bibio</i> sp.	X	X							
Empididae: <i>Iteaphila</i> sp.		X							
<i>Rhamphomyia</i> sp.		X							
Clythiidae: gen. et sp. indet.		X							
Syrphidae: <i>Syrphus opinator</i> O. S.		X	X	X	X	X	X		
Anthomyiidae: <i>Pegomya</i> sp.	X	X							
<i>Hylemya alcaethae</i> Walk.		X	X	X	X	X	X		
<i>Hydrotaea militaris</i> Mg.		X	X	X	X				
Calliphoridae: <i>Phormia terrae-nova</i> Desv.		X	X	X	X				
<i>Calliphora vomitaria</i> L.	X	X	X	X	X				
Lepidoptera									
Geometridae: <i>Melanolopia imperfectaria</i> Walk.	X	X							
<i>M. imitata</i> Walk.	X	X							
<i>Mesoleuca gratulata</i> Walk.	X								
<i>Trichodesia californiata</i> Pack.		X							

TABLE 4 (Cont.)

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Hymenoptera									
Tenthredinidae: <i>Tenthredo</i> sp...		X							
<i>Pristola macnabi</i> Ross.....		X							
Ichneumonidae: <i>Ephialtes</i>									
<i>clapiae</i> (Harr.).....			X	X	X				
Belytidae: <i>Xenotoma</i> sp.....	X	X	X	X	X	X	X		
Vespidae: <i>Vespula vulgaris</i> L....		X	X	X	X	X			
<i>V. rufa</i> var. <i>consobrina</i>									
(Sous.).....		X	X	X	X	X			
Bombidae: <i>Bombus sikkimensis</i>									
Nyl.....		X	X	X	X	X			
<i>B. flavifrons dimidiatus</i>		X	X	X	X	X			
Total.....	9	43	43	24	18	20	3	8	1

by more frequent north and east winds, although the predominating wind direction is still from the southwest. Wind velocity is moderate, though averaging higher than that in any other season. Light intensity averages 35% of full sunlight, a marked increase over that of any of the winter seasons. Average weekly precipitation is below that of the emergine sector. An increase of evaporation rates in the vernal aspect is to some degree correlated with decreasing humidity. Vapor pressure deficits are increasingly high, average weekly maxima in general being greater than .200 mm Hg.

Prevernine Sector: The prevernine (early) sector is characterized by the blossoms of skunk cabbages (*Lysichiton camtschatensis*), violets (*Viola sempervirens*), Oxalis, huckleberries and trilliums.

The aspect opens with evidences of increased vertebrate activity. Tracks and sign of deer were noted more frequently. The rufous hummingbird (*Selasphorus rufus* (Gmelin)) was the first spring migrant bird noticed. Bears (*Ursus americanus altifrontalis* (Elliot)) become active at the same time that the skunk cabbages blossom. Chipmunks at this elevation are regularly first heard about this time, following some three months of almost complete dormancy. Moles and *Microtus* become consistently active near the surface of the soil. Higher temperatures permit the amphibia to become active; the discoglossid toad (*Ascaphus truei* Stejneger) and salamanders (*Ensatina eschscholtzii* Gray and *Plethodon vehicularis* Cooper) appearing frequently on the forest floor.

Molluscs, represented by humped slugs (*Prophysaon* spp.) and the Columbia snail (*Polygyra columbiana pilosa* (Henderson)), are first consistently recorded on the humus surface during this sector. A white geometrid moth (*Mesoleuca gratulata* Walk.) is particularly conspicuous in this sector. Psychodidae here attain a peak in abundance and then suddenly disappear from the records during the late sector. Tenthredinidae are present during the prevernine sector, and their larvae become noticeable in the late sector. Aleyrodidae imagoes disappear during the prevernine sector, while *Pegomya* closes its period of activity at this time to reappear in another brood in the late autumn.

The vernal aspect begins when the average maxi-

mum weekly temperatures jump from the vicinity of 50° F, or below, to the vicinity of 60° F, or above (Fig. 15). A leveling off or an actual slump in temperature occurs subsequent to the first ascent, and when the temperature rises the second time a weather change brings in the vernine sector. Precipitation averages 1.35 in./wk, considerably less than that of the emergine sector of winter. Wind velocity during the prevernine sector is the highest of the year, but varying within the season as well as from year to year.

Vernine Sector: The vernine sector or late sector of the vernal aspect brings false Solomon's-Seal, Oregon grape, salmonberry (*Rubus spectabilis*), vanilla-leaf, twayblade and devil's club (*Oplopanax horrida*) into bloom.

This sector is usually marked by the appearance of summer resident birds. Their arrival may possibly be characteristic of the entire vernal season although the exact arrival dates were hard to determine. In some years the first records of some species were in the prevernine sector. The more important summer resident birds of this locality are the russet-backed Swainson thrush (*Hyloichia usutulata* (Nuttall)), the western wood pewee (*Myiochanes richardsoni* (Swainson)), Pacific western flycatcher (*Empidonax difficilis* Baird), the hermit warbler (*Dendroica occidentalis* (Townsend)) and the Pacific band-tailed pigeon (*Columba fasciata monilis* Vigors). Birds are nesting and mammals are rearing families during this sector.

The beginning of this late sector of the vernal aspect is quite clearly indicated by the first appearance of the large, snail-eating carabid *Scaphinotus angusticollis nigripennis* Roesch. A larger white geometrid (*Trichodesia californiata* Pack.) takes the place of *Mesoleuca*, blue-bottle flies become very conspicuous and Empidae appear consistently and in numbers (Table 4). The myriapod (*Harpaghe haydeniana* (Wood)) reaches a peak of abundance on the humus surface in this period.

The vernine maximum weekly temperature averages at least 60° F. It may briefly be considerably higher, but tends to range near that point. Precipitation averages 1.03 in./wk. Wind velocity is less than during the prevernine sector and predominantly southwest. Light intensity is higher in the vernine than in the prevernine sector, while vapor pressure deficits are also usually higher.

AESTIVAL ASPECT

The aestival aspect is the last one which can be characterized in this coniferous region by the blossoming of plants, and is also distinguished by the fruiting of a number of herbs and shrubs. The aestival aspect is 2-2.5 months in length. The dates at which the season begins and ends are somewhat variable, the extremes for the beginning date being May 25, 1936 and June 24, 1937, with August 13, 1933 the earliest, and August 30, 1937 the latest, dates marking the termination.

TABLE 5.* Meteorological data for the vernal aspect—seasonal averages.
PV—prevernine sector; SV—vernine sector; T—entire aspect.

	1933			1934			1935			1936			1937			Average		
	PV	SV	T	PV	SV	T	PV	SV	T	PV	SV	T	PV	SV	T	PV	SV	T
Temperature																		
Maximum	51.3	61.5	53.5	61.4	68.5	65.5	47.6	64.1	55.9	58.3	73.3	64.7	48.2	65.0	58.9	53.3	66.5	59.1
Minimum	33.1	36.0	33.7	39.4	40.9	40.2	32.0	38.1	35.0	39.2	40.0	38.2	33.0	39.2	37.0	35.4	38.8	36.8
Mean	42.2	48.3	43.5	51.4	54.7	53.5	40.6	51.1	45.9	48.7	56.8	52.2	41.0	52.1	48.0	44.9	52.7	48.5
Range	18.1	25.5	19.7	22.0	27.7	25.3	15.2	26.0	20.2	19.0	33.0	25.0	15.0	25.0	21.8	17.4	27.4	22.4
Relative Humidity																		
Maximum	93.4	93.7	93.6	86.8	84.5	85.5	96.0	95.6	95.7	90.0	91.0	90.4	92.4	85.4	88.3	90.8	89.4	90.2
Minimum	67.1	61.7	65.9	45.0	41.0	42.8	63.5	37.1	45.8	57.0	36.0	48.0	74.4	45.4	58.3	55.3	43.7	49.8
Mean	87.4	89.5	88.1	73.3	70.8	72.0	90.3	77.6	81.8	80.5	77.4	79.3	89.6	85.2	87.1	83.2	76.7	79.8
Range	25.6	32.0	26.0	28.0	43.5	42.2	32.6	58.5	49.8	33.0	55.0	42.4	27.4	42.5	33.9	34.3	45.6	40.1
Precipitation	2.07	0.80	1.71	1.71	0.70	1.06	0.35	0.69	0.61	0.24	2.15	1.06	2.71	0.74	1.56	1.35	1.03	1.20
Light	34.2	33.3	34.0	32.0	30.8	32.0	28.0	32.5	53.3	41.4	28.0	32.8	31.5	31.6	35.6	34.6
Evaporation	4.50	5.29	4.90	5.14	5.78	5.35	2.12	5.16	3.43	5.98
Vapor Pressure Deficit																		
Maximum	.121	.188	.141	.266	.345	.311	.133	.331	.271	.205	.336	.270	.081	.286	.200	.161	.237	.238
Mean	.032	.026	.029	.107	.109	.108	.025	.046	.041	.065	.086	.074	.025	.093	.064	.048	.060	.059

*See notes for Table 3.

From a faunal standpoint, the aestival and vernal aspects are similar, with a large variety of species, many of which are common to both. The aestival aspect has, however, its own distinctive fauna. Scorpion flies (Mecoptera) were recorded only from this aspect, *Cercopidae* (*Philaenus leucophthalmus*) also characterize the period, while aphids attain their peak of abundance and variety. Cicadas also seem to be characteristic here, as they were heard trilling in the tree tops, though none was collected. Coleoptera are less abundant than in the vernal aspect, constituting only 29.4% of the common species. The aestival insects are preponderantly diptera (44.4%). Several species of diptera common to the vernal aspect were forced to drop out or become insignificant in the aestival aspect, while 20 genera, with over 27 species, were added, producing a decided increase in the variety of diptera represented in the aestival as compared with the vernal aspect. The increase was especially noticeable in the predaceous and blood-sucking groups, 12 out of the 35 common species of diptera in this aspect being haemophagous, contrasting with the pollenophagous species characteristic of the vernal aspect. The Anthomyidae, Calliphoridae, Muscidae and Tipulidae increased in diversity. Geometrid moths were represented by two genera peculiar to the aestival season. The variety of organisms active in the upper layers during the season was high. As many as 35 important families of insects were taken on one collecting date, with an average of 15-20 for each collection period during the season (Fig. 10). 78 species of insects were common and conspicuous during the aestival aspect. Half of these species were restricted to the aestival aspect, occurrence of the remaining 50% being distributed in both directions from the aestival peak (Fig. 16, aestival), 30.7% of aestival species occurring in the vernal aspect and

32% in the autumnal aspect. Over half (56.4%) of the aestival species occurred in both sectors, 24.4% occurring only in the cisaestine sector and only 18.1% being restricted to the aestine sector. The cisaestine sector has the highest total of characteristic insects for the year, 64 species. A few species (14.1%) first appear in one of the aestival sectors and continue into the autumnal aspect or beyond. These are mostly diptera. Few of the aestival species occur in the hiemine and none occurs in the hibernine sector. The large red mites of the humus surface (Trombididae) are the only characteristic invertebrates other than insects. Amphibia apparently aestivate during this aspect as they were not observed moving about on the surface.

The aestival aspect as a whole is a season of high temperatures and vapor pressure deficits, with a correspondingly high population curve. Meteorologically, this season gives a false impression of stability. The range of temperatures is wider at this season than at any other, even though temperatures fluctuate at a high level and show comparatively little variation in either maximum or minimum levels. Precipitation during the aestival aspect reaches the lowest point for the year, averaging 0.2 in./wk for the 5 years. The humidity is much higher than the low precipitation would seem to warrant, the mean maximum averaging 98% for the 5 yrs and the mean minimum 46%. Wind velocity is low during this aspect with northwest and southwest, light to moderate winds equally represented. Light intensity averages higher than in the vernal aspect (39%). Vapor pressure deficit reaches a very high point during this aspect, weekly maxima averaging over .350 mm Hg. Evaporation in general is maintained at a high level. Hygrothermograph records are especially distinctive during this aspect, the diel rhythm of temperature and humidity fluctuations being very regular (Fig. 11d).

TABLE 6. Insects characteristic of the aestival aspect (summer). Explanation as in Table 2.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Neuroptera									
Hemerobiidae: <i>Hemerobius conjunctus</i> Fitch.....				X	X				
Mecoptera									
Panorpidae: <i>Brachypanorpa oregonensis</i> McLach.....				X	X				
Corrodentia									
Caeciliidae: <i>Caecilius aurantiacus</i> Hgn.....					X	X	X		
<i>C. quillayute</i> Chap.....					X	X	X		
Homoptera									
Cercopidae: <i>Philaenus leucophthalmus</i>				X	X				
Aphididae: <i>Macrosiphum solanifolii</i> (Ashm.).....				X	X				
<i>M. scolopii</i> Essig.....				X	X				
<i>Amphorophora rubicola</i> (Oestl.).....				X	X				
Coleoptera									
Carabidae: <i>Scaphinotus angusticollis nigripennis</i> Roesch.....			X	X		X	X		
Cantharidae: <i>Podabrus piniphilus</i> Esch.....			X	X					
<i>Silis pallida</i> Mann.....				X					
Cephaloidea: <i>Cephaloon pacificum</i> Van D.....				X					
<i>C. bicolor</i> Horn.....				X					
Mordellidae: <i>Anthobates</i> sp.....				X	X				
Elaterridae: <i>Ctenicera umbripennis</i> (Lec.).....			X	X					
<i>C. sylvatica</i> (Van D.).....					X				
<i>Athous rufiventris</i> Esch.....					X				
<i>A. vittiger</i> Lec.....					X				
<i>A. pallidipennis</i> Mann.....					X				
<i>Megapenthes stigmoseus</i> (Lec.).....					X				
Lucanidae: <i>Platyceroidea laticollis</i> (Cay.).....				X					
<i>P. aeneus</i> (Van D.).....				X					
Cerambycidae: <i>Plectura spinicollis</i> Mann.....		X	X	X	X	X	X	X	
Chrysomelidae: <i>Syneta simplex</i> Lec.....				X					
<i>Luperodes</i> sp.....				X					
Cureulionidae: <i>Sciopithes obcurus</i> Horn.....		X	X	X	X	X	X	--	
<i>Nemocetes incomptus</i> Horn.....		X	X	X	X	X	X	--	
<i>Dytobus lecontei</i> Cay.....				X	X	X			
<i>Stremneus tuberosus</i> Boh.....				X	X				
Scolytidae: <i>Pseudohylesinus grandis</i> Sw.....				X	X	X	X		
<i>Gnathotrichus sulcatus</i> (Lec.).....				X	X	X	X		
Diptera									
Tipulidae: <i>Cylindrotoma splendens</i> Doane.....				X	X				
<i>Limnophila oregonensis</i> Alex.....				X	X	X			
<i>Tipula macnabi</i> Alex.....				X	X	X	X		
Simuliidae: <i>Prosimulium fulvum</i> Coq.....				X	X				
Tendipedidae: <i>Chasmatonotus univittatus</i> Lw.....				X	X				
Heleidae: <i>Culicoides</i> sp.....				X	X	X	X		
Culicidae: <i>Aedes varipalpus</i> Coq.....				X	X	X	X		
<i>Culiseta incidens</i> (Thoms.).....	X	X	X	X	X	X	X		
Fungivoridae: <i>Platyura</i> sp.....				X	X	X			
<i>Euphrasyne</i> sp.....				X	X				
Tabanidae: <i>Tabanus californicus</i> Marten.....					X				
<i>T. captonis</i> Marten.....					X				
<i>T. sonomensis</i> O. S.....					X				
<i>T. atrobasis</i> McD.....					X				
<i>Chrysops praeivus</i> O. S.....				X					
<i>C. pertinax</i> Will.....				X					

TABLE 6 (Cont.)

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Rhagionidae: <i>Rhagio costalis</i> Lw.....				X	X				
Leptidae: <i>Symphoromyia plumbea</i> Ald.....				X	X				
<i>S. kincaidi</i> Ald.....				X	X				
Cyrtidae: <i>Eulonchus sapphirinus</i> O. S.....				X					
Syrphidae: <i>Stenocrphus rectoides</i> Cur.....			X	X	X				
<i>Syrphus opinator</i> O. S.....		X	X	X	X	X			
<i>Melanostoma angustatum</i> Will.....				X	X	X			
Piophilidae: <i>Mycetulus costalis</i> Mel.....				X	X				
<i>M. bipunctatus</i> Fall.....				X	X				
Helomyzidae: <i>Suillia aestivilis</i> Lw.....				X	X	X	X		
Anthomyiidae: <i>Hylemya alcaethae</i> Walk.....		X	X	X	X	X	X		
<i>Alloctylus diaphana</i> Wd.....				X	X	X	X		
<i>Helina lysiniae</i> Walk.....				X	X	X	X		
<i>Fannia incisurata</i> Zett.....				X	X				
<i>Fannia ochrogaster</i> Mall.....				X	X				
<i>Hydrotea militaris</i> Mg.....			X	X	X	X			
Muscidae: <i>Mezembrina latricellae</i> Desv.....				X	X	X			
Calliphoridae: <i>Phormia terrae-novae</i> Desv.....		X	X	X	X	X			
<i>Calliphora vomitoria</i> L.....		X	X	X	X	X			
Lepidoptera									
Geometridae: <i>Ceratodalia queneata</i> Pack.....				X	X				
<i>Hydriomena oedenata</i> Swett.....				X					
<i>H. captata</i> Swett.....				X					
Hymenoptera									
Belytidae: <i>Pantocius</i> sp.....				X	X				
Ichneumonidae: <i>Ephialtes ellopiae</i> (Harr.).....			X	X	X				
<i>Amblyteles rufatus</i> (Cress.).....				X					
<i>A. astutus</i> (Hgn.).....				X					
<i>A. semiasis</i> (Cress.).....				X					
Vespididae: <i>Vespula vulgaris</i> L.....		X	X	X	X	X	X		
<i>V. maculata</i> (L.).....		X	X	X	X	X			
Bombidae: <i>Bombus sitkensis</i> Nyl.....		X	X	X	X	X			
<i>B. flavifrons dimidiatus</i>		X	X	X	X	X			
Total.....	1	12	25	64	59	28	14	3	0

The aestival aspect, like the other aspects, is divided into sectors, though not quite so clearly. The break between the cisaestine and aestine sectors comes at about the middle of the aestival aspect but varies considerably from year to year, the extremes being July 1, 1934 and August 4, 1937.

Cisaestine (L. cis, on this side, and L. aestus, summer) *Sector*: The cisaestine or early sector of the aestival aspect is characterized by the blooming of Clintonia, salal, Coralorrhiza and false Solomon's-seal. Salmonberries mature in this sector and are practically gone before the end of the aspect.

Scaphinotus remains active during the cisaestine sector, disappearing at its close, while a group of beetles including the Cantharidae, Lucanidae and Cephaloidea are limited to this sector. In the diptera, Tabanidae of the genus Chrysops and the Cyrtidae (*Eulonchus sapphirinus*) are restricted to this

TABLE 7.* Meteorological data for the aestival aspect—seasonal averages.

CA—cisaestine sector; SA—aestine sector; T—entire aspect.

	1933			1934			1935			1936			1937			Average		
	CA	SA	T	CA	SA	T	CA	SA	T	CA	SA	T	CA	SA	T	CA	SA	T
Temperature																		
Maximum	68.8	72.4	70.0	67.0	69.1	68.3	70.0	79.0	72.8	70.8	72.4	71.6	75.2	77.3	76.1	70.0	74.0	71.7
Minimum	44.3	47.2	45.7	44.0	48.7	47.0	42.2	48.6	45.7	46.0	48.8	47.5	48.5	48.0	48.2	45.0	48.2	46.8
Mean	56.2	60.8	58.5	55.0	59.0	57.7	56.2	62.7	57.6	58.5	61.3	60.0	61.6	62.6	62.0	57.4	61.2	59.1
Range	22.5	26.0	24.2	23.0	20.0	21.3	28.0	30.4	29.3	24.8	22.1	23.1	26.7	29.3	27.5	25.0	25.5	25.0
Relative Humidity																		
Maximum	84.5	83.0	83.1	90.0	90.0	90.0	95.0	95.5	95.5	93.3	90.1	91.7	86.5	88.0	87.0	89.8	88.2	89.2
Minimum	53.0	39.8	43.5	44.6	48.8	47.0	41.0	50.4	47.6	43.1	55.6	50.4	46.8	28.0	41.6	46.1	44.5	46.1
Mean	70.6	64.2	66.4	72.0	74.5	73.4	84.3	75.0	79.7	82.0	75.7	79.1	72.7	69.0	71.3	74.3	71.7	73.9
Range	31.5	43.2	39.8	45.4	41.1	42.9	54.0	44.6	55.1	48.1	34.5	41.3	39.6	60.0	46.4	43.7	46.6	43.1
Precipitation	0.61	0.04	0.32	0.14	0.08	0.12	0.35	0.11	0.23	0.61	0.10	0.33	0.45	0.35	0.42	0.42	0.13	0.28
Light	26.0	42.0	34.0	36.0	32.0	34.0	57.0	27.4	40.0	32.0	60.0	46.0	40.0	43.3	41.1	38.3	40.9	39.0
Evaporation	10.8	6.02	4.82	5.31	7.67	8.07	7.97	4.22	7.07	5.75	8.32	8.19	8.27
Vapor Pressure Deficit																		
Maximum	.349	.396	.376	.353	.309	.325	.369	.420	.396	.324	.326	.325	.386	.344	.372	.354	.359	.358
Mean	.056	.173	.139	.122	.119	.120	.092	.120	.106	.072	.131	.101	.129	.134	.132	.094	.135	.119

*See notes for Table 3.

sector. The cisaestine sector has a somewhat greater total of characteristic insects than the following (aestine) sector (Table 6 and Fig. 13). It is in general cooler and cloudier than the aestine sector but the evaporation rates and vapor pressure deficits do not differ significantly.

Aestine (L. aestus, summer) Sector: About the middle of the aestival aspect, the false Solomon's seal and Clintonia fruits add a touch of color to the forest herb layer. Leptidae, psocids and Hemerobiidae are characteristic of the late sector of this aspect, their appearance usually coinciding with the opening date. The Leptidae disappeared consistently with the close of the aspect. The russet-backed Swainson thrush, western wood pewee, hermit warbler and Pacific bandtailed pigeon leave during the aestine sector.

The aestine sector is characterized by high temperatures and low humidity, high vapor pressure deficit, low precipitation and high light intensity (Table 7). It usually draws to a close with an extremely hot, dry period in which the temperatures frequently reach or exceed 80° F and humidity descends to 40% or even 30%. This is usually succeeded by attainment of high maximum humidity (sometimes accompanied by the first light, fall rains), and continued high maximum temperatures as the serotinine sector of the autumnal aspect begins.

Autumnal Aspect

As the aestival aspect closes, the accompanying population shift initiates the autumnal decline toward the limited population of winter. By this time, the annual destiny of plant life has been fulfilled. Most fruits have formed and expendable vegetative parts are deteriorating. During the autumnal aspect the meteorological transition toward the unfavorable physical conditions of winter begins, with decreasing light

intensity and increasing humidity being the earliest expression of their approach. The autumnal aspect as a whole occupies 2-2.5 months, beginning some time in August and ending in late October or mid-November in most years.

The autumnal aspect in this community, like other aspects, consists of more than one subseason. Most investigators of faunal aspection agree with the conclusion that the fall season is composed of two phases which they have called the serotinal and autumnal. There are indications that certain authors have interpreted a serotinal season as starting about where the mid-aestival break in population occurred in this study, so it is difficult to tell whether the term serotinal as they have used it refers to a late summer or early fall season. Their term autumnal clearly applies to the fall aspect as a whole. The early sector of the autumnal aspect is here designated as the serotinine and the later sector the autumnine.

A drop in faunal population at the close of the aestival aspect initiates the autumnal aspect (Fig. 10). The serotinine and autumnine sectors are closely related biotically. The difference in faunal composition of these two sectors is much less than that between the aestine and serotinine sectors, especially as to diversity of insects (Tables 6 and 8). 67 species of insects are characteristic of the autumnal aspect, 55% appearing for the first time within the aspect and 15% reappearing after a period of inconspicuousness or complete absence. 25% of autumnal insects occur only in the autumnal aspect, 18% being limited to the serotinine sector and 12% to the autumnine sector. Much of the autumnal population is also found in other aspects (Fig. 13, autumnal). The vernal fauna includes 27% of the autumnal species, as does the aestival population, while 22.2% of the autumnal insects occur also in the hiemal aspect. The nature

and activities of the vertebrate population also unite the serotinine and autumnine sectors into a fall aspect. The summer resident birds have departed and permanent residents and fall migrants tend to occur in flocks in both fall sectors. The smaller mammals are more active than during the middle of the summer. The larger mammals indicate restlessness by roaming through the forest before being limited by the more rigorous weather of the winter. Amphibia are active in both sectors. While the autumnal sectors are clearly two parts of a single season, the differences between the two are somewhat greater than those between the sectors of most other aspects (Table 9).

Serotinine (L. *Serotinus*, late ripe) **Sector:** The average length of the serotinine sector is only 5 weeks, usually starting late in August and giving way to the autumnine sector in early October. There is a tendency for it to be abbreviated in those years in which the autumnine sector is long.

The serotinine is the sector in which the last fruits become ripened. Oregon grape and salal mature at this elevation early in the sector and the last red huckleberries ripen. False Solomon's-seal also bears fruit well into this sector. The herbs show aging by yellowed, ragged leaves which are being attacked by mildew and other fungi (Fig. 7).

The renewed fall activity of *Scaphinotus* probably provides as good a positive index to the early phase of the autumnal aspect as any part of the faunal picture. Cicadellidae (*Empoasca* sp. and *Conodonus flavicapitatus* Van. D.), were also good indicators of the beginning of this season. The first fall records of Aleoerodidae approximated the opening dates in the last two years of the study, when the most careful observations were made. Termites were recorded as emerging in their nuptial flights at this time in the two years in which the winged forms were observed. The serotinine sector is the first in which more invertebrates drop out of the population than are added to it. This decrease in variety principally affects the diptera and coleoptera. The insects present appear to be hardy types that find conditions suitable for constant activity; accordingly the population curve representing the variety of families stays at a high level. Coleoptera, which were so abundant in the vernal and aestival seasons, become very limited in variety in the serotinine sector. Diptera continue to dominate the field in variety. Among the lepidoptera, geometrids are active in the serotinine as in the aestine sector, but all are unfamiliar genera and species. The pine-white butterfly (*Neophasia menapii* Feld.) and the hemlock looper moth (*Nepitia phantasmaria* Stkr.) are species of potential economic significance. The former is characteristic of the first few days and the latter of the entire sector. Yellow-jackets reach a peak in abundance and activity during this sector and toward its close become very irritable and inclined to sting. Mosquitoes are also troublesome and numerous at this time. An abundance of adult spiders characterizes the serotinine sector; they are at the height of their predatory activity (Table 8).

The vertebrate fauna is characterized by renewed

TABLE 8. Insects characteristic of the autumnal aspect (fall). Explanation as in Table 2.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Collembola									
Entomobryidae: <i>Tomocerus</i>									
<i>flavescens</i> Tullb.	X	X	X	X	--	X	X	X	
Sminthuridae: <i>Ptenothrix</i> sp.	X	X	X	X	--	X	X	X	
Isoptera									
Kalotermitidae: <i>Zootermopsis</i>									
<i>angusticollis</i> Hgn.						X			
Corrodentia									
Caceliidae: <i>Cacelius</i>									
<i>aurantivacus</i> Hgn.				X	X	X			
<i>C. guilayute</i> Chap.				X	X	X			
Neuroptera									
Hemeroptera: <i>Hemerobius</i>									
<i>biatrigatus</i> Bks.				X	X				
<i>H. pacificus</i> Bks.				X	X				
<i>H. humilis</i> L.				X	X				
<i>H. conjunctus</i> Fitch.				X	X				
Homoptera									
Coccinidae: indet.	X						X	X	X
Aleyrodidae: gen. et sp. indet.	X	X	X			X	X	X	--
Fulgoroidea: <i>Catonia nemoralis</i>									
Van D.						X	X		
Cicadellidae: <i>Empoasca</i> sp.						X	X	X	
<i>Empoasca filamenta</i> Del.							X	X	
<i>Colladonus flavicapitatus</i>									
(Van D.)						X			
Coleoptera									
Carabidae: <i>Scaphinotus</i>									
<i>angusticollis nigripennis</i>									
Roesch.			X	X		X	X		
Staphylinidae: <i>Anthobium</i>									
<i>picatum</i> Fauvel.		X					X	X	
<i>A. subcostatum</i> Maekl.		X					X	X	
Derodontidae: <i>Pellastica</i>									
<i>tuberculata</i> Mann.							X		
<i>Derodontus trisignatus</i> Mann.							X		
Elatidae: <i>Hemicrepidius</i>									
<i>morio</i> Lec.						X			
Cerambycidae: <i>Plectrura spinicauda</i> Mann.		X	X	X	X	X	X	X	
Cureulionidae: <i>Sciopithes</i>									
<i>obscurus</i> Horn.		X	X	X	X	X	X	--	
<i>Nemocetes incomptus</i> Horn.		X	X	X	X	X	X	--	
Scolytidae: <i>Gnathotrichus sulcatus</i> (Lec.)			X	X	X	X			
Diptera									
Tipulidae: <i>Tipula macnabi</i>									
Alex.			X	X	X	X			
<i>Ormosia fusiformis</i> (Doane)						X	X		
<i>O. perpedabilis</i> Alex.						X	X		
Psychodidae: <i>Psychodes</i> sp.	X	X	X			X	X	X	X
Helicidae: <i>Culicoides</i> sp.				X	X	X	X		
Culicidae: <i>Aedes varipalpus</i>									
Coq.				X	X	X			
<i>Culiseta incidens</i> (Thoms.)	X	X	X	X	X	X	X		
Fungivoridae: <i>Lycoria</i> sp.					X	X			
<i>Bolitophila</i> sp.					X	X			
<i>Ezechia</i> sp.	X	X					X	X	X
<i>Fungivora</i> sp. 1.	X	X				X	X	X	
<i>Polyzona</i> sp.						X			
Anisopidae: <i>Anisopus</i>									
<i>alternatus</i> Say.							X		
<i>A. punctatus</i> Fab.							X		
Empidae: <i>Hormopeza nigricans</i>							X	X	
Syrphidae: <i>Syrphus opinator</i>									
O. S.		X	X	X	X	X			
Helomyzidae: <i>Suilla assimilis</i>									
Lw.				X	X	X	X		
Anthomyiidae: <i>Pegomya</i> sp.	X	X						X	
<i>Hyalemya alcaethae</i> Walk.		X	X	X	X	X	X		
<i>Alloctylus diaphana</i> Wd.				X	X	X	X		
<i>Helina lyinae</i> Walk.				X	X	X	X		
Muscidae: <i>Mesembrina</i>									
<i>latrillae</i> Desv.					X	X	X		

TABLE 8 (Cont.)

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Calliphoridae: <i>Calliphora</i>									
<i>tomitoria</i> L.		X	X	X	X	X			
<i>Phormia terraenovae</i> Desv.			X	X	X	X			
Tachinidae: <i>Arctophyto</i>									
<i>sarcophagina</i> Coq.					X	X			
<i>A. wickhami</i>					X	X			
Phoridae: <i>Megaselia</i> sp. 1.						X	X		
<i>Megaselia</i> sp. 2.						X	X		
Lepidoptera									
Pieridae: <i>Neophasia menapii</i>									
Feld.						X			
Geometridae: <i>Nepytia phantas-</i>									
<i>maria</i> Stkr.						X			
Tortricidae: <i>Peronia britania</i>									
Kearf.						X			
Gracillariidae: <i>Cameraria gaul-</i>									
<i>therella</i> Wlsh. adult.						X			
<i>C. gaultherella</i> Wlsh. larvae.	X	X					X	X	X
Hymenoptera									
Belytidae: <i>Xenotoma</i> sp.	X	X	X		X	X	X		
<i>Miela</i> sp.						X			
Vespididae: <i>Vespula vulgaris</i> L.		X	X	X	X	X	X		
<i>V. maculata</i> L.		X	X	X	X	X			
<i>V. rufa consobrina</i> (Saus.)		X	X	X	X	X			
Ichneumonidae: <i>Thaumato-</i>									
<i>typidea</i> sp.							X		
Braconidae: <i>Apanteles longi-</i>									
<i>cornis</i> (Prov.)							X		
Eulophidae: <i>Tetrastichus</i> sp.							X		
<i>Polynura</i> sp.							X		
Total	11	21	19	21	30	50	44	12	3

activity of amphibia in response to the higher humidity and early fall rains. The summer resident birds are gone and varied thrushes, red crossbills, chickadees and kinglets occur in flocks which pass over and through the forest in waves of intense activity. Renewed activity of moles and *Microtus* becomes evident as they throw up fresh mounds of earth and make ridges in the humus. Chipmunks are more frequently heard and seen.

The close of the serotinine sector is marked sharply by the disappearance of the large muscid fly (*Mesembrina latriellei* Desv.) which coincides with the end of this sector in each of the 5 yrs. Other blue-bottle flies (*Phormia* spp.) also disappear at the close of this sector. The activities of the yellow-jackets (*Vespula vulgaris* L.) also tend to diminish at this time. The treehole mosquito (*Aedes varipalpus* Coq.) usually ceased being bothersome at the close of the serotinine sector.

In the serotinine sector the average of temperatures for five years is slightly higher, and the minimum temperatures slightly lower, than those of the aestival aspect (Table 10). The apparent stability of aestival temperatures is breaking down. Though the weekly maximum drops lower than in the aestival aspect, there are frequently records of over 80° F early in this aspect. The average minimum temperatures, which during the aestival aspect and early serotinine sector fluctuate close to the annual mean of 50° F, fall permanently below that level toward the latter part of the serotinine sector (Fig. 15). Precipitation

increases again in this sector, especially toward its close, leading into the rainy autumnine sector. There is a tendency toward great oscillation in the curves of mean and minimum humidities, short humid periods alternating with exceptionally dry intervals. Wind velocity is practically the same as in the aestival aspect and predominantly southwest. Light intensity is lower throughout the autumnal aspect than in the aestival, due to the smoke of forest fires and haze characteristic of the serotinine sector, and the effect of clouds and fog in the autumnine sector, when it is even lower. Records for evaporation rates and vapor pressure deficit indicate that there is not much difference in the desiccating effects of the aestival and serotinine sectors, in spite of the increased humidity and precipitation in the latter. Hazard stick data also show that the increased precipitation and humidity of the serotinine sector has not built up the moisture content of the logs. The close of this sector appears to be governed more by a drop in temperatures than by any other physical factor.

Autumnine (L. autumnus, autumn) Sector: In extent, this sector is the most abbreviated of all. It generally begins early in October and lasts to approximately the first week of November.

The increased dampness of this sector brings out fungus fruiting bodies and their associated mycetophagous fauna in humus and decaying wood. It is the season of falling leaves. The herb layer, which in the serotinine had begun to die, in this sector has lost any vestige of life. The leaves instead of being yellow have become mottled dark brown with decay. All of the deciduous shrubs and trees lose their leaves at this time. The vine maples, especially, lose their leaves in steady showers as the sun strikes them in the morning following a frost. Even the conifers join in showering the forest floor with wornout needles.

Consistent with the opening of the autumnine sector are the appearance of a brown scale (not identified) on the leaves of salal and Oregon grape and the occurrence of fresh leaf-miner tunnels in salal leaves. In spite of the brevity of this sector, its population is distinctive. There is enough dry, sunny, warm weather to produce considerable activity among hardy types of insects. Braconidae, Ichneumonidae and Vespidae are particularly noticeable. Otherwise, diptera dominate the community as usual. Several types of coleoptera are present, including the mycetophagous Derodontidae and Staphylinidae. The Trichoceridae return (Table 8). The disappearance of Scaphinotus marked the end of the season in all years except 1935. In that year an unusually early snowfall accompanied by exceptionally low temperatures brought the aspect to a close abruptly. Rising temperatures later brought out two isolated specimens that were probably only indicative of a potential extension of the autumnal season.

The bird population is rather stable during the autumnine sector, consisting wholly of permanent residents, except for the flocks of juncos (mostly *Junco hyemalis oreganus* (Townsend)), which drift through

TABLE 9.* Seasonal averages of meteorological data for the autumnal aspect.
S—serotinine sector; A—autumnine sector; T—entire aspect.

	1933			1934			1935			1936			1937			Average		
	S	A	T	S	A	T	S	A	T	S	A	T	S	A	T	S	A	T
Temperature																		
Maximum.....	77.0	61.5	67.0	71.0	58.3	64.6	73.1	66.3	70.8	71.4	57.0	65.4	70.5	63.2	67.6	72.6	61.2	67.1
Minimum.....	50.1	42.8	45.5	56.5	40.3	43.4	49.0	44.3	47.4	46.7	38.8	43.4	48.5	43.5	46.4	48.1	41.9	45.0
Mean.....	63.6	52.4	56.3	58.7	49.4	54.0	61.0	55.3	59.1	59.0	47.9	54.4	58.0	53.4	56.1	60.0	51.6	56.1
Range.....	26.7	18.5	21.5	24.5	17.6	21.0	24.1	22.0	23.3	24.7	16.2	22.0	22.0	19.2	15.4	24.4	19.1	21.8
Relative Humidity																		
Maximum.....	90.8	92.6	91.9	90.2	89.0	89.5	95.2	95.6	95.3	92.2	91.2	91.0	91.4	91.7	91.5	91.9	92.0	91.8
Minimum.....	42.0	67.0	55.5	41.5	63.7	54.8	42.6	51.3	43.5	34.8	41.0	37.4	51.5	68.0	56.6	42.5	58.2	49.5
Mean.....	67.5	81.0	68.7	62.7	80.0	73.1	71.5	80.5	77.5	68.6	73.9	70.8	77.6	84.3	81.5	69.5	79.9	74.3
Range.....	47.2	25.0	35.5	42.2	25.3	34.9	52.8	44.3	49.6	57.4	50.2	54.4	39.8	23.7	34.0	49.2	35.7	41.6
Precipitation.....	0.36	1.47	0.80	0.24	3.60	2.07	0.28	0.59	0.38	0.20	0.14	0.17	1.04	1.41	1.19	0.42	1.44	0.92
Light.....	37.5	26.6	31.0	21.0	24.2	23.3	35.0	10.7	21.6	30.0	40.0	32.6	45.0	21.6	35.0	33.7	24.6	30.3
Evaporation.....	9.53	3.30	6.12	6.46	2.36	4.22	8.96	3.16	4.23	5.80	4.68	3.37	5.64	2.15	4.35	7.27	3.13	4.45
Vapor Pressure Deficit																		
Maximum.....	.458	.147	.197	.462	.129	.280	.420	.158	.333	.377	.227	.321	.330409	.165	.282
Mean.....	.178	.071	.110	.191	.077	.122	.155	.045	.153	.143	.086	.112	.097	.061	.087	.152	.069	.116

*See notes for Table 3.

TABLE 10. Meteorological data summarized by aspects—averages for the period of the study.

	Hiemal Aspect			Vernal Aspect		Aestival Aspect		Autumnal Aspect	
	H	Hi	E	PV	SV	CA	SA	S	A
Temperature (°F.)									
Maximum.....	50	44	49	53	67	70	74	73	61
Minimum.....	34	28	33	35	39	45	48	48	42
Mean.....	44	36	40	45	53	57	61	60	52
Range.....	17	16	16	17	27	25	25	24	19
Relative Humidity (%)									
Maximum.....	93	92	94	91	89	90	88	92	92
Minimum.....	74	83	75	55	44	46	45	43	58
Mean.....	87	90	91	83	77	74	72	70	80
Range.....	19	9	19	34	46	44	43	49	34
Precipitation.....	2.73	2.90	2.17	1.35	1.03	0.42	0.13	0.42	1.44
Light (%).....	26	25	24	32	36	38	41	34	25
Vapor Pressure Deficit									
Maximum.....	.077	.040	.067	.161	.297	.355	.359	.409	.165
Mean.....	.040	.020	.024	.048	.060	.094	.135	.152	.069
Wind Velocity (mi./day).....	18	16	16	23	19	18	19	17	20

the mountains in the course of their southward migration. Chipmunks attain a peak of abundance in our records at this time and amphibia reach a second peak of activity. Deer are mating and bear wander restlessly preceding hibernation.

The autumnine sector is a season of the first fall frosts, heavy rains and strong winds, interspersed with Indian summer weather. The first snowfall may also occur during this sector. Light intensity drops decidedly. Evaporation is slightly less in this season than in the preceding and correlates in a rough way with the precipitation for the various years. The increased precipitation and relative humidity of the

autumnine sector definitely lower the vapor pressure deficit (Table 10). A fall in weekly maximum temperature below 55° F, usually accompanied by heavy precipitation—which at this level may be in the form of snow—together with minimum temperatures of 40° F or less, brings the autumnal aspect to a close.

DISCUSSION

SUBSTANTIATION OF SECTOR CONCEPT

Comparison of the seasonal boundaries of faunal and floral aspection established by other investigators with those of the Coast Range is of interest (Fig. 16). The moderate climate of the Pacific Coast greatly

abbreviates the dormant stage of the winter aspect, which is marked by transitional stages at both ends, therefore the author has subdivided the hiemal aspect, using the terms, *hibernine* for the dead of winter, *hiemine* for the introductory winter season, and *emergenine* for the transitional stage preceding the spring aspect. Such a subdivision establishes sectors of a duration in harmony with the extent of aspectional subseasons throughout the rest of the year. The length of the hiemal aspect of other authors is quite extensive as compared with the remaining seasons of the year. This season extends from approximately two and a half months as determined by Shackleford (1934) for an Oklahoma prairie, to over five months indicated by Smith (1928) in seral stages of an Illinois forest, by Fichter (1942) for Nebraska prairie, and by Brown (1931) for the oak-hickory forests of Wisconsin. A 5-month hiemal season is quite a contrast to the brevity of their prevernal and vernal seasons which generally last only one month. An extremely long hiemal season is no doubt partly justifiable on the basis of the comparatively long winters characteristic of mid-continental areas. Some interesting evidence for the division of the hiemal aspect into hiemine, hibernine and emergenine sectors, however, appears in the papers of several of the ecologists who have considered aspection in the deciduous forest and prairie biomes.

In spite of the widely separated locations, the usual beginning date for the hiemal aspect occurs in November. The population curve shown by Weese (1924) contains an indication of an early phase of the hiemal aspect (hiemine sector of the present paper) in an elm-maple forest in Illinois. He reports a period of about a month between November 14 and December 19 in which the total population is still declining to its minimum average for the winter. Williams (1936) described November as the time of hibernation for invertebrates and some vertebrates and states that in December, January and February the species list of birds is restricted to the permanent resident and winter visitor groups. The intimation that the bird population is not entirely restricted until December perhaps shows that a pre-hibernal subdivision should be recognized. Adams (1941) also may have indicated something of the same kind when he referred to an abundance of *Ptenothrix* on November 27 and December 4, 19, and 25 after the hiemal aspect had begun. Shackleford's (1929) curve of weekly mean air temperatures for 1926 shows that air temperatures did not drop much below 32° F until about the middle of December, which should permit enough invertebrate activity above the soil level to mark a season preceding the dead of winter, when hibernation is most nearly complete.

The greater part of the hiemal aspect reported by other investigators correlates well with the season referred to as *hibernine* in this paper. The animals are for the most part in an inactive state, but, as recognized in most reports, a few insects and spiders are active on warm days throughout the winter.

The evidence from other authors that an emergenine sector should be separated from the latter part of the hiemal aspect is even better. The total population curve shown by Weese (1924) does not show it unless it should take the place of his prevernal aspect, which is one month earlier than Weaver & Fitzpatrick's (1934) average prevernal aspect in the prairie at almost the same latitude. The prevernal aspect might then apply to the more rapid increase in population reported by Weese during the early part of April. The appearance of late winter and spring mosses mentioned by Weaver & Fitzpatrick may be a floristic indication of an emergenine sector in the prairie. The notable increase in bird population reported by Twomey (1945) during the latter part of his hiemal aspect is coincident with the beginning of the migration of hibernating insects from beneath the leaves of the ground stratum, and probably represents an emergenine phenomenon. Cantlon (1953) suggests an emergenine type of phenomenon when he refers to Wolfe *et al.* (1949) in stating, "The change from winter to spring has been defined as the period when vegetative activity shows a marked increase near the surface and under the litter." A sudden and sustained increase in *Parasitus* sp., together with *Epitrix fuscula*, and *Gongylidiellum pallidum*, from the latter part of February to early April in Smith's (1928) report probably indicates a potential emergenine sector or at least a prevernal sector, although the latter would probably not be comparable to the length reported by Davidson (1930) and Williams (1936) (Fig. 16).

Weese (1924) reported a rise of the weekly mean air temperatures to between - 2.1 and 8.3° C during March in the latter part of this hiemal aspect, which corresponds to the temperature range between 30° and 50° F reported for the emergenine sector in this paper. Shackleford (1929) also indicates a sharp rise in weekly mean air temperatures above 32° F about the first of February, 1927, which is another evidence of an emergenine sector.

Additional evidence for an emergenine sector is shown in the graphed population and environmental factors for the prevernal season by Davidson (1932), in which the mean air temperature records remained below 30° F until the first part of April. This could mark the close of an emergenine sector. A sharp rise in temperature followed in the latter part of her prevernal season, which brings the average, with one lapse below 32° F, to a figure well above that point. Such a sudden rise in temperature would mark a true prevernal season. Positive evidence of a faunal nature for an emergenine sector is shown in Davidson's data by the early rise of the spider, *Gongylidiellum pallidum* Em., to a peak of abundance between the first of February and the first of April. Renewed activity during this period is indicated for the perennial predominant spiders. Another seasonal spider, *Phrurolithus palustris* Bks., also originates in the middle of her prevernal season. These evidences point to a break in the season she called prevernal, which could

be recognized as evidence for an earlier emerginine and a later prevernine season.

The great length of the prevernal season as reported by Carpenter (1935), Williams (1936), and Davidson (1930) is probably due to the inclusion of an unrecognized emerginine sector. Although Carpenter starts the prevernal on February 15 on the basis of the "arrival of the first spring birds" and "appearance of *Peziza* cups and budding of the buckeye and elm," he states, "By April 2 the aspection had greatly progressed with the weekly mean temperature rising to 46.5° F as compared with 33° for the preceding week"; and further, "On the later date (April 2) many Diptera were flying and first ground blossoms appeared." Such a statement clearly indicates a cleavage in the middle of his prevernal aspect. The criteria for aspection from a botanical point of view are indicated by Weaver & Clements (1938) in their statement, "Societies in forests are found only beneath the primary layer of trees and their subdominance is obvious." Since Carpenter reports the earliest "ground blossoms" to be those of herbs, April 2 would seem to mark the actual beginning of the prevernal aspect in his studies and would give a seasonal duration for that aspect comparable to that reported by the majority of investigators considered in Figure 16.

Williams (1936) indicates precisely the same phenomenon by stating that the prevernal aspect begins with the month of February, in spite of his statement that "most of its aspects are hibernal." The early part of the prevernal season he characterizes botanically by renewed color of mosses and lichens and faunally by renewed bird activity. He then notes that late in March the earliest flowers come into bloom.

Thus on almost the same dates two investigators (Carpenter and Williams) on different projects, in widely separated localities, indicate that a prevernal season might be recognized as beginning in accord with the plant ecologists' concept, *i.e.*, that the earliest blossoms mark the opening of the prevernal season. The author believes that the hiatus between the dead of winter and the plant ecologists' prevernal season should be recognized and designates it the emerginine sector. This term fits the indications of renewed activity of plant and animal life referred to above (from about the first of February to approximately the last of March). The prevernal aspect of all investigators, except Davidson (1930), who unfortunately did not designate in her paper the bases for dating this season, would then be brought into close approximation as to dates and duration.

The prevernine sector of this Oregon locality corresponds in duration to the prevernal aspect of some other investigators (Fig. 16, Weaver & Fitzpatrick, Pound & Clements, Weese, Shackleford, Twomey, and Adams). Most investigators have reported the vernal season as one of the shortest, though Pound & Clements, as well as Weese and Williams, each allotted two months to it. The research on Saddleback Mountain in the Coast Range reveals a tendency for the

early spring (prevernine) and late fall (autumnine) sectors to be pinched down into very brief periods. This is also shown by the serotinal season as reported by Adams.

The aestival aspect compares most favorably in duration and dates included for the locations listed in Figure 16. The effect of the latitude of regions, as well as annual variations in climate, would seem to account for the discrepancies that occur. For example, the aestival aspect is reported by Brown as starting in April in the oak-hickory woods in Oklahoma, the only case in which this season is indicated as starting so early. This locality is about five degrees farther south than the places where seasonal studies were made in Illinois and Nebraska, which could account for the earlier aestival season in Oklahoma. In the study by the author in the Coast Range forests, the aestival aspect includes the greater part of the month of August and begins at a later date than those given to this season by most other investigators. The later dates here can be explained by the fact that the writer's station was located on approximately the 45th parallel of north latitude. The fact that the elevation selected in the Coast Range mountains is greater than that of Illinois and the central states in general would accentuate the tendency for the seasons to be later at this latitude than in the vicinity of the 40th parallel where most other projects were located. There is little doubt about the aestival character of the season as a whole when compared with the aestival aspects of other authors, even in cases where they do not indicate a subdivision of this aspect.

The fall seasons as illustrated in Figure 16 show that the period Brown (1931) designated as a serotinal aspect coincides with Shackleford's (1934) aestival season (in the same state at about the same latitude). It seems likely that Brown has given a preferable interpretation of the season, since the mid-portion of her serotinal aspect coincides with dates ascribed to the serotinal aspect by other authors. In her study of an Illinois prairie (1929), Shackleford apparently divided the period others have called a serotinal aspect equally between the aestival and autumnal seasons, as have Muma & Muma (1949) in their study of the spider fauna of three eastern Nebraska communities. The inclusive interpretation of the term *autumnal* as used by recent authors (*e.g.*, Shackleford, Weaver & Fitzpatrick, and Fichter) is antedated by Pound & Clements' (1900) use of the term *serotinal* for the entire fall period. When the serotinal and autumnal seasons of most eastern authors are combined, their total duration of approximately three to four months is roughly comparable. This is from about a week to over one month longer than the combined duration of the serotinine and autumnine sectors of the autumnal aspect in the Coast Range location in Oregon. It appears that the autumns may be of greater length in the central states than on the Pacific Coast.

Tabulations such as Figure 16, though they reveal

interesting parallels, also reveal a prevailing lack of agreement upon seasonal dates and terminology, even where the same communities have been studied. It seems likely that many of the differences are not inherent in the communities, *i.e.*, not due to annuation but are subjective, due to differences in the observers and to the relatively indefinite seasonal criteria which have been used.

INTERRELATIONSHIPS OF SEASONS

Examination of Table 10 reveals that the hiemine, hibernine and emerginine sectors are closely united from an environmental standpoint. They have an almost identical average temperature range for the 5 years. A 5-yr average of relative humidities produces about the same result. Precipitation averages show a high rate for all three sectors together. Vapor pressure deficit averages, which have been shown to correlate with the curve of population (Fig. 10), tend to split this winter group of biotic seasons into sectors. The three winter sectors are united biotically by the occurrence of three groups of diptera.

The prevernine and vernine sectors of the vernal aspect are in many ways similar or complementary to the autumnine and serotinine sectors of the autumnal aspect, respectively. In some ways the entire vernal aspect strikes a balance with the autumnine sector of fall. In others the prevernine sector of the vernal aspect compares most favorably with the autumnine sector and the vernine sector with the serotinine sector (Table 10). Certain environmental factors unite the prevernine sector with the summer, while the autumnal aspect also tends to be pulled two ways—toward the summer or toward the winter season. The vertebrate populations of the vernal and autumnal seasonal societies are alike in the peak of activity attained by the amphibia in both seasons. Birds and mammals are also very active in both. The seasons differ, however, in the type of activity exhibited. The birds in the vernal aspect are numerous due to an influx of summer residents. In the autumnal aspect the summer residents are gone, but winter residents are traveling in flocks and surges of bird activity traverse the forest as these flocks pass through. In the vernal aspect the reproductive activities of mammals render the mammalian fauna relatively conspicuous. In the autumnal aspect, especially the late sector, a pre-hibernal restlessness causes local migration of larger mammals, and hoarding activities among many of the smaller ones. Twomey (1945) apparently noted the same phenomenon when he writes that "the vernal and autumnal aspects are comparable in that they both show great fluctuations in the respective animal populations." He refers to the vernal aspect as "one of intense activity" and says that the "most striking phenomenon of the autumnal period is that of movement both in the insects and birds."

Both the environmental line of cleavage and biotic distinctions between the vernal and aestival aspects are striking. Vegetational differences are not as clear

as faunal differences, as the herbs and shrubs continue to blossom, and fruits do not appear to characterize this area until the late sector of the aestival aspect. The evidence of a decided change in the biota between the vernal and aestival aspects is supported by the addition of many new families of insects to the aestival aspect. This picture of a major break between the vernal and aestival aspects is also aided by the activities of summer resident birds, their conspicuous courting activity during the vernal aspect contrasting with their quieter nesting activities during the early sector of the aestival aspect, which Twomey (1945) designates as a change "from one of song to silence."

The similarity of the aestival aspect to the serotinine sector of the autumnal aspect is largely environmental. Despite a close relationship of the environmental factors the insect fauna is very distinctive (Tables 6 & 8). The vertebrates, like the insect groups, tend to emphasize the dissimilarity of the aestival and autumnal aspects. A break in the biotic structure of the community, due to simplification of the insect and bird population and revival of mammalian and amphibian activity, marks the end of the aestival and beginning of the autumnal aspects as the point where decline toward the winter season of limited activity and variety of fauna begins.

The organization of the biotic seasonal societies recognized in this study places the aestival aspect in contrast to the hiemal aspect. In many ways the aestival aspect is well qualified to fill this role. It is characterized by the highest minimum temperatures, lowest weekly precipitation and greatest intensity of light. The population in this aspect attains its peak in number and diversity of fauna. As was indicated in the detailed description, there is good evidence that an early and late phase of this biotic season should be recognized. When this is done, and the aestival aspect is divided into early and late sectors, it resembles the spring and fall aspects in being a two-phase biotic unit comparable to the unit formed by the vernal aspect with its prevernine and vernine sectors. The serotinal and autumnal aspects of other authors could be considered to be early and late sectors of a fall aspect, the environmental and biotic characteristics of which are transitional between the summer and winter seasons.

Thus the seasonal relationships revealed by this study, and the classification adopted here serve to emphasize the basic fact of the complementary nature of the aestival aspect (summer, or the growing season) and the hiemal aspect (winter, or the dormant season), as well as the transitional nature of the vernal aspect (spring) and the autumnal aspect (fall). It represents a return to the basic simplicity of the four astronomical seasons of the temperate zone, coupled with a recognition of the inherent complexity of each of the major seasons.

SUMMARY AND CONCLUSIONS

1. A 5-yr aspectional study was conducted from 1933 to 1938 at an elevation of 1400 ft in a sublimax

community of mature, even-aged Douglas fir and hemlock, in a location representative of conditions at an average elevation in the mesophytic coniferous biome along the crest of the Coast Range Mountains.

2. Collections and observations were made at weekly intervals. Continuous records were made of the temperature in the humus layer of the soil surface and temperature and humidity in the low shrub layer, while maximum and minimum thermometers at shrub, low tree and high tree levels, and instruments measuring evaporation, wind velocity, precipitation, light intensity and moisture content of wood in the shrub and herb layers, were read weekly. For this aspectional study only results obtained from the layers above the soil surface have been considered.

3. A curve of population for each of the 5 years of investigation was constructed on the basis of the number of families of insects collected, or observed to be active, in the layers above ground each week. Besides the fluctuating, gradual and continuous increase of the population to a summer maximum, and similar decrease to a winter minimum, striking changes were found to occur at varying intervals, contributing a new aspect to the population. These changes in population were both quantitative and qualitative. The locations of these major fluctuations in the normal curve of population growth or decline were used as indications of seasonal boundaries.

4. Fluctuations of environmental factors, which are not always the same or in the same degree, usually accompany the major biotic fluctuations.

5. An environmental factor derived from averaging the vapor pressure deficit at the time of collection, with the mean daily maximum vapor pressure deficit for the preceding week, and the light intensity of the collection date, correlates well with the curve of diversity of insect population above the ground level.

6. Biotic seasons can and should be determined by means of vegetational, faunal, and environmental criteria. (1) Vegetational criteria include the blooming and fruiting of plants, especially subdominants, the formation of new growth, and the defoliation of the plant community. (2) Of particular importance under faunal criteria, are the shifting composition of the population, peaks of abundance of animals in the various stages of their life histories, reproductive activities, and migrations, both horizontal and vertical. Composition of the insect population is especially important. (3) Among environmental criteria, temperature, humidity, evaporation and precipitation are of classic importance in establishing seasonal limits, while vapor-pressure deficit, which is based on temperature and humidity and hence correlated with the evaporating power of the air, is of particular value. This study revealed a correlation between a combined vapor pressure deficit—light factor and diversity of insect population. The distinctive seasonal patterns of temperature and humidity as recorded by the hygrothermograph are of significant use, while weather in the larger sense, including wind, clouds,

barometric pressure, storms, etc., must also be considered.

7. The term *aspect* has been reserved to denote the four major biotic seasons, corresponding roughly to the four astronomical *seasons*, winter, spring, summer, and fall, which are bounded by the equinoxes and solstices. *Sector* designates the biotic subdivisions of the four major aspects, the suffix *-ine* being used in preference to the *-al* suffix heretofore used for both major and minor biotic seasons. The seasons are (1) hiemal aspect (winter) with hiemine, hibernine, and emerginine sectors; (2) vernal aspect (spring) with prevernine and vernine sectors; (3) aestival aspect (summer) with eisaestine and aestine sectors; and (4) autumnal aspect (fall) with serotinine and autumnine sectors. (a) The three sectors of the hiemal aspect are closely related both environmentally and biotically. (b) Hibernine is reserved for the subdivision of the hiemal aspect characterized by deepest dormancy of animals, particularly arthropods, and of all plants, while the hiemine and emerginine sectors are recognized as separate sectors, during which organisms are entering and emerging from dormancy, respectively. (c) The vernal and autumnal aspects exhibited marked biotic and environmental similarity and both are transitional. (d) The vernal and aestival aspects are separated by a major line of cleavage, which is most clearly marked by environmental data, but is also evident biotically. (e) The aestival aspect is divided into two sectors, chiefly on the basis of biotic criteria. Maximum variability of the insect population in the eisaestine sector is correlated with the favorable environmental factors of that period. (f) Environmental correlation of the late aestival (aestine) and early autumnal (serotinine) sectors is very close but a biotic comparison shows great differences between the two. (g) The serotinine sector marks the beginning of the autumnal decline toward environmental and biotic aspects characteristic of winter.

8. The distinctive composition of any sector is produced by the loss of a group of animals characteristic of the close of the preceding sector, the presence of an intrinsic group, and the addition of a group of animals which carries through into the following sector.

9. Interpretations of aspectional criteria can be sufficiently specific to enable comparison of locations varying in elevation, latitude and other topographic or geographic features.

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SUMMARY AND INTERPRETATION OF UNDERGROUND DEVELOPMENT IN NATURAL GRASSLAND COMMUNITIES

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INTRODUCTION

Root development in grassland has been studied many years. A survey of the underground plant parts in the Palouse Prairie of southeastern Washington was made in 1913-14. The work was continued under the auspices of the Carnegie Institution of Washington in the prairies and plains of central North America. Investigations were made at more than 25 stations in Colorado, Kansas, Nebraska, and South Dakota, from the Missouri River to the Rocky Mountains. Roots of practically all of the grassland dominants were examined, many in different communities. The total number of root systems examined was about 1,500 and the results were published in 1919-20. The objectives of these early studies were to ascertain the general relationships of roots to soil and to each other as regards spread, depth, and degree of development in the same community and in different and widely separated communities. They were exploratory.

Extensive studies on the structure of grassland communities were continued. Root systems were further examined as supplementary to Experimental Vegetation (1924), Plant Competition (1929), The Prairie (1934) and various other studies. The great drought of 1933-40 in both prairie and Great Plains offered an exceptional opportunity to ascertain the responses of native plants to extremely adverse environmental

conditions. The role played by root systems in endurance of and recovery from drought was thoroughly investigated. Meanwhile notable contributions on root studies had been made by Sperry on Illinois prairie (1935), Albertson on the hard lands of west-central Kansas (1937), Tolstead on the Sand Hills (1942) and Hopkins on the Loess Hills of Nebraska (1951). In all these studies the trench and pick method was employed. "While the trench method is slower and more tedious than that of root washing, it has so many advantages and gives such superior results that the additional effort is amply justified" (Sperry, 1935).

With the rapid development of soil science and much emphasis on the role of grasses in soil formation and stabilization, a distinct need arose for a better understanding of the intimate relations of roots and soil. A new method was devised—the monolith method—for securing a representative sample of an entire root system (Weaver & Darland 1949). By this method a section of soil may be obtained from a trench wall to the depth of the grass roots without disturbing the root patterns. Usually a sample 12 in. wide and 4-6 ft in depth is taken to a thickness of 3 in. in the trench wall. When soaked for many hours, the soil may be gently washed away. The root system remains without vertical displacement. The number of roots, degree of branching, distribution and weight

at any depth or in any soil horizon may be ascertained. By this method many dominant grasses and the soil in which they grew have been restudied, more carefully and completely.

With a renewed interest in the ecology and physiology of root distribution of grasses in their relations to soils and removal of tops in grazing, the following summary and interpretation has been written. The past half-century has offered advantages for the study of natural grasslands and their environments which the future can not offer because of over-grazing, too frequent mowing, use of herbicides, reseeding, etc., and especially plowing. Indeed the eastern prairies were almost destroyed before they were investigated by ecologists.

This study includes the True Prairie of the western third of Iowa, which extends westward to about 98°30' west longitude in Nebraska, and the Mixed Prairie of the Great Plains, westward and southwestward to the Rocky Mountains in Colorado. Communities of grasses of lowland and upland prairie will be presented first and then those of the hard lands, loess hills, and sand hills of the Great Plains. The usual root habits of several dominants are shown in community charts for each of the several major plant communities as they occurred on well-developed and stabilized soil. These furnish a basis for the comparison of other grasses of the same or different communities. An attempt is made to relate the community root habit to the soil conditions and aerial environment under which the vegetation developed.

The physical or chemical causes of variations in root development in certain soil types are considered as well as the relation of root development to removal of tops, as in frequent mowing or various degrees of grazing.

Both common and scientific names of grasses are according to Hitchcock & Chase (1950) revised Manual of the Grasses of the United States.

GRASSLAND SOILS

The well-drained and well-developed zonal soils of the grasslands of Nebraska, Kansas and Colorado comprise chiefly four great groups. These are the Prairie soils of the humid grasslands, the black earths or Northern Chernozems of the subhumid grasslands, the Chestnut or Northern Dark-Brown soils of the semiarid grasslands, and, farther westward, the still lighter-colored Northern Brown Soils. Associated with each of the zonal soils are other soils (intra-zonal). Some are young with only the beginnings of soil development (azonal soils), some have excessively developed claypan subsoils (Planosols), and still others are poorly drained and marshy but without claypans (Wiesenboden) (*cf.* Marbut 1935, Kellogg 1936).

True Prairie occurs mostly on zonal Prairie soil but it extends westward on Chernozems for many miles. Prairie soils are very dark brown in color, rich in organic matter, especially in the upper portion, moderately to strongly acid in reaction, and

well supplied with nutrients necessary for a luxuriant development of grass. They have been leached to the extent that they do not have a horizon of calcium carbonate.

Chernozem soils occupy the most humid part of the drier region having soils with a calcium carbonate horizon. These deep, black soils are, owing to the luxuriant growth of grasses, high in content of organic matter distributed deeply throughout. They are neutral in reaction and even more fertile than Prairie soils, but productivity is less because of decreased precipitation.

Both Prairie soils and Chernozems are rich, deep, and fertile. Silt loams prevail with unusually good texture and structure. There are nearly always enough large pores to insure adequate drainage and good aeration and enough small ones to offer an adequate water-holding capacity. In various soil types under prairie grass total pore space usually composes about 50% of the soil volume. The mellow, granular topsoil (A horizon), enriched by untold generations of grasses and forbs, extends usually to depths of 12 to 18 in. Beneath is a zone of higher clay content and lighter in color (B horizon) which extends to a depth of about 3 to 4 ft. Underlying the solum is the parent material of the C horizon. It is often yellowish or at least lighter in color than the solum, partly because of its lower content of organic matter and partly because it is rich in lime. Except for rock outcrops, the parent material extends many feet in depth. Although lime has been eluviated from the A horizon and at least the upper portion of the B horizon, the soil (in this western area) is neutral or only slightly acid, since a constant supply of lime is brought to the surface by the grasses and deposited there when they die (*cf.* Thorp 1948).

Dark-Brown and Brown Soils are described later together with the Mixed Prairie vegetation which they support.

UNDERGROUND PARTS OF GRASSES OF LOWLAND TRUE PRAIRIE

The two types of grassland of greatest importance and widest extent in true prairie are those characterized by little bluestem and big bluestem, respectively. Prairie of the wetter or more moist lowlands is dominated by grasses that are quite different from those typically forming upland communities. A description of the 3 major prairie communities of lowland and the 3 of upland, together with their composition and structure, has been recorded (Weaver & Fitzpatrick 1934). A more succinct statement may be found in North American Prairie (Weaver 1954).

A map showing the lowlands along the Missouri River and its tributaries, the smaller streams and ravines leading into them, and the well-watered lower slopes of hills, would include the portion of the area formerly dominated by big bluestem and other lowland grasses. Exceptions are woodlands, marshes, soil covered with water or deep deposits of sand. Almost pure stands of big bluestem (*Andropogon ge-*

ardi) occurred over extensive areas in which this grass alone composed 70 to more than 90% of the vegetation.

BIG BLUESTEM

Total basal cover of big bluestem, even in the best stands, averaged only about 13% of the soil surface. Growth is rapid; a dense stand of foliage 3 ft high is produced by midsummer. Then stout stems, each with 9 to 10 leaves, extend upward; the mature flower stalks in late summer reach heights of 6 to 10 ft.

The very abundant roots of mature plants extend downward almost vertically. A few may run off somewhat obliquely before turning downward. They are rather coarse (1-3 mm in diam.) and tough. Although well supplied with laterals 2-6 in. in length, branching is not so profuse as on roots of upland grasses. Depths of 6 to 7 ft are usually attained.

Figure 1 and the following community charts show the average number of roots in an inch width of soil as ascertained at each foot in depth in the trench wall and from soil monoliths taken from many different trenches. Where the roots are too numerous in the upper soil to be shown in the drawing, this is indicated in the legend. Root depth of each grass is an average of 10 to 20 samples from widely separated sites in each of the plant communities illustrated. Relative size of roots of various grasses is also shown. Lateral spread of roots (the radial distance to which roots extend from the base of the plant) is shown as far as space permits. Only enough detail has been added to indicate the branching habit. Branches, as regard length, are drawn to scale. Intermixing of roots of plants (except in Fig. 4) has been avoided for the sake of clarity.

The rhizomes of big bluestem are coarse, usually 3-6 mm thick, much branched and frequently continuous for distances of 6-10 in. or more. Their general level is about 1 to 2 in. below the soil surface, but they are common to a depth of 4 in. The rhizomes alone form a rigid, coarse, open network, which is anchored by the multitude of coarse, branched roots arising from them. They are studded above by the abundant coarse stem bases 1-2 in. of which are buried in the soil. The whole stem-rhizome-root system forms a magnificent network for holding the soil against erosion by flooding (Fig. 2).

The amount of underground materials of big bluestem to a depth of 4 in. was ascertained in 24 widely distributed prairies. Each sample consisted of 0.5 sq m (5.38 sq ft) of soil, from which the underground parts were recovered by washing away the soil. The material was oven-dried at 100°C.

The portion of the true prairie examined extended from Guthrie Center and Creston, Iowa, approximately 75 mi east of the Missouri River, to Nelson, Nebraska, about 200 mi southwestward (Fig. 3). The silt loam soils are all deep and of high fertility. Rate of evaporation is increasingly greater from east to west, while other conditions favorable to growth, such as water content of soil, gradually decrease.

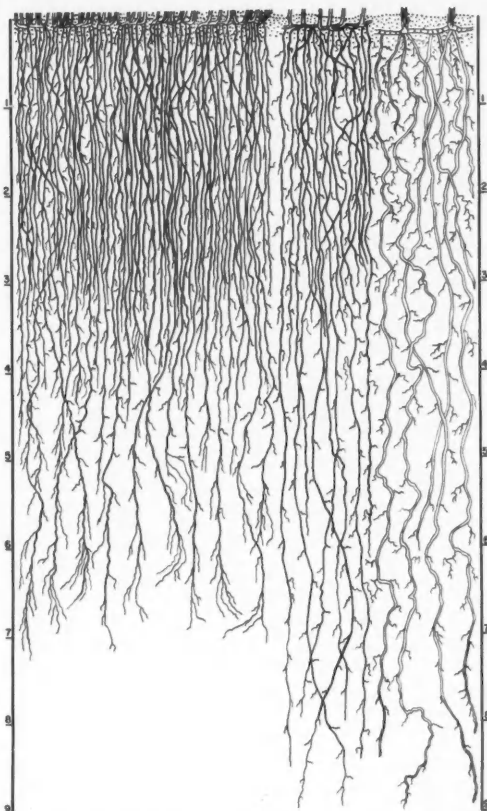


FIG. 1. Characteristic development of roots and rhizomes of grasses occurring in the big bluestem community. (Left) big bluestem (*Andropogon gerardi*), switchgrass (*Panicum virgatum*), and prairie cordgrass (*Spartina pectinata*) (right). Both vertical and horizontal scale in feet. The average number of roots in the first inch of soil in the trench wall is shown, except in the first 2 ft under big bluestem. Foliage height in midsummer is 3-4.5 ft and mature plants are 6-10 ft tall.

Yield data from stations with approximately equal rainfall were grouped and the average weights expressed in T/A. At the 6 Anita stations, mostly in southwestern Iowa, the rainfall averaged 32 in.; at the 8 Lincoln stations, in south eastern Nebraska, it was 29 in.; and at the Nelson stations, it was only 26 in. The yields of plant materials were 4.54, 3.54 and 3.17 T/A, respectively (Shiveley & Weaver 1939).

Average weight of roots occurring at 4 to 12 in. depth at Lincoln was about one-third the total weight of underground parts in the 0-4 in. level (4.1 T) or 1.35 T.

Root weight decreases rapidly with depth, especially below 24 in. However, the importance of the subsoil is demonstrated by the relatively great quantity of roots found there. An oven-dry weight of more than 300 lbs/A of grass roots often occurs in

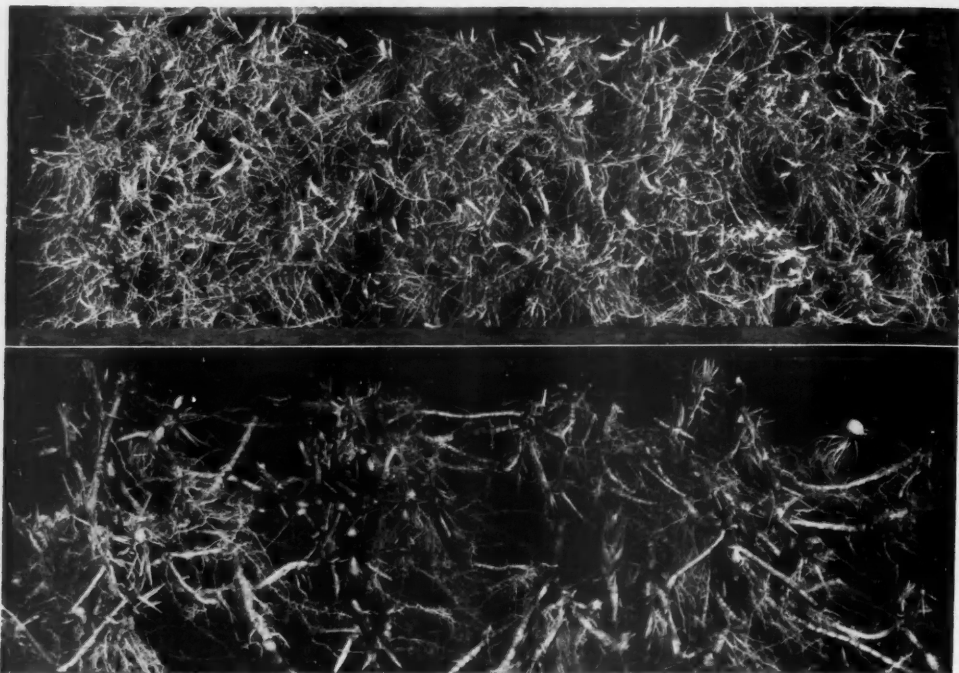


FIG. 2. (Upper) Underground parts of big bluestem from .5 sq m (5.38 sq ft) to a depth of 10 cm (4 in) from Union, Nebraska, after the soil was washed away. Note the uniform distribution of roots. (Lower) Roots and rhizomes of prairie cordgrass. Note wide spacing of stems as shown in Figure 1. Only 1% of the soil surface was occupied by stems, yet dense shade excluded nearly all other plants.

the fourth foot of bluestem prairie soil. These deeper roots probably absorb quite out of proportion to their small weight.

The rate of production of the large quantities of roots has been ascertained. Big bluestem was grown from seedlings to maturity without competition and under an environment favorable for its development. Fifty seedlings were grown in the field in each of 3 steel drums (58 gal., 3 ft. deep) placed in the soil. The first year the grass produced 48% of its mature root weight. The second year it added 34% more, and the third summer the remaining 18%. Thus, it reached approximately its maximum root development in 3 years. The underground materials produced were similar in amount to those ascertained earlier in typical mature stands in native prairie (Weaver & Zink 1946).

The length of life of individual roots of several grasses was ascertained by banding large numbers of young roots of each species. Narrow bands of aluminum or soft tin were used. All roots remained alive on big bluestem and switchgrass (*Panicum virgatum*) for a period of 2 yrs, and the loss by death was only about 20% for big bluestem at the end of the third growing season. This loss was almost negligible, since at this time an average of 882 roots per plant had been produced (Weaver & Zink 1946a).

Finally the rate of decay of roots and rhizomes in their natural environment when the plants were killed

was ascertained. Relative resistance to decay varied with the species. Decomposition proceeded at about the same rate at all soil levels. Big bluestem and Indian grass (*Sorghastrum nutans*) decayed rather slowly. A few roots retained some tensile strength after 3 yrs. Switchgrass decayed somewhat more rapidly. Rhizomes of these and other grasses were neither more or less resistant to decay than the roots (Weaver 1947).

OTHER GRASSES

Indian grass is usually associated with big bluestem and like it is a sod former. Its abundance is variable, increasing southward, but over the central lowlands as a whole it composed only 1 to 5% of the grass population. The roots are not so coarse as those of big bluestem nor do they usually extend quite so deep, but they are often branched more abundantly.

Prairie cordgrass (*Spartina pectinata*) occurs in pure stands only in soils that are too wet and consequently too poorly aerated for big bluestem. The coarse stems of this sod-forming grass usually attain a height of 6 to 10 ft. Both rhizomes and roots of prairie cordgrass are much larger than those of big bluestem and they also occur at greater depths (Fig. 1). The coarse, woody, much branched rhizomes, form an open network in part or all of the first foot of soil (Fig. 2). The roots are usually 3-5 mm in diameter. They grow from the rhizomes and the

interrupted, especially in the second foot, by heavy rains. The available supply usually ranged between 5 and 15% at the depths (about 5 ft) occupied by grass roots. On the lowland, available water content was 3 to 10% greater in the surface foot and often 5 to 11% in excess of that on the upland in the deeper soil. A water table occurred at about 10 ft.

A similar study in 1932 of water-content of upland and lowland prairie on the flood plain of the Missouri River south of Union, Nebraska, gave even greater differences. Here big bluestem roots extended to a depth of 7 ft in Wabash clay loam. The water table occurred at about 10 ft. During this year of approximately average rainfall the surface 6 in. always had available water and at greater depths the amount was usually about 13% or more. Repeated sampling through many years revealed this to be about the usual condition, a continuous but rarely excessive water supply on lowland.

Growth in lowland prairie is rapid. Big bluestem elongates at a maximum rate of nearly 0.75 in./day and, like the other tall grasses, completes its vegetative growth late in July. Then the flower stalks begin to develop, often elongating 1.5-3 in./day, and the plants reach heights of 6-10 ft. Prairie cordgrass and sometimes Indian grass are taller, but switchgrass is often somewhat less in height. All except Canada wild-rye, which flowers in midsummer, are warm season grasses adapted to a long growing season.

This magnificent cover of grasses presents by midsummer a foliage surface of 5-10 A/A of soil. Since the grass roots are not only perennial but long-lived, the plants may absorb at all depths throughout the growing season. The abundant supply of water offsets the enormous losses by transpiration. The roots also take up sufficient nutrients to permit a yield of 3-5 T/A of forage annually. It is believed that lack of lateral spread of roots in the surface soil results in part from the abundance of moisture and partly from the network of rhizomes which distributes the roots widely and uniformly. Moreover, lowland soils are in general of a more uniform structure than are those of uplands. This, with their continuously higher water content, enables roots to penetrate through them easily and uniformly. The great depth that roots attain may be related to the usually increasing water supply with depth and the great demands of these tall grasses for water and nutrients. Many lowland soils have water tables within reach of very long roots.

It may well be that the continuously greater supply of water in the wetter habitats of switchgrass and especially prairie cordgrass is an environmental condition reflected in the more open network of rhizomes and fewer roots than those of big bluestem.

The amount of water absorbed and transpired in the big bluestem community must be very great. Yet only once (in 1934) during the past half century has drought in lowlands been observed to interrupt the growth of the grasses in late July. Then big bluestem was wilted and half dried. Switchgrass was al-

most as dry and even prairie cordgrass, discolored and dwarfed to less than half its normal stature, showed great distress. But these grasses were rarely killed where they were rooted in deep loam soils. The absence or lack of abundance of upland grasses is not due to unfavorable soil conditions but to the dense shade produced by big bluestem. When it is removed, they thrive.

UNDERGROUND PARTS OF GRASSES OF UPLAND TRUE PRAIRIE

Upland prairie is quite different from that of lowland. The grasses are nearly all bunch grasses of the mid-grass type, with heights ranging between 2 and 3.5 ft. Upland soils are not usually sufficiently moist to promote development of tall grasses, especially in competition with more xeric species.

LITTLE BLUESTEM

Andropogon scoparius is the principal grass of the uplands. It forms not only the most extensive communities of upland but also occupies an area over the prairie as a whole many times as great as that dominated by big bluestem. It exceeds in abundance all other grasses combined, and usually constitutes 55% and sometimes 90% of the vegetation in this area. It ordinarily forms an interrupted sod of mats and tufts but large bunches prevail in drier places. The average basal cover is about 15%. The foliage varies in height in late summer from 7-12 in. on dry uplands but it is 15-18 in. in more favorable sites. Flower stalks vary in height from 1.5-3 ft. Usually it fruits abundantly only in wet years.

The mature root system consists of a vast network of roots and masses of finely branched rootlets, some more than 30 in. in length and branched to the third order. The largest roots have only about one-third the diameter (0.5 to 1 mm) of those of big bluestem. The soil beneath the crown and several inches on all sides of it is threaded with dense mats of roots to a depth of 4 to 5 ft (Fig. 4). The large number of roots in a 1-in. layer of trench wall below 2 ft is from an average of many counts. Actually some roots entered this layer from soil removed in digging the trench or from behind the exposed face of the trench wall. Approximately an equal number grew outward from it. This is difficult to illustrate, hence all of the roots are shown as if they grew only within this inch of soil throughout their entire length, as most of them did.

Stem bases and surface roots firmly bind the soil in the mats or bunches. Most of the space between bunches is also occupied by a dense network of roots.

Samples of sod were taken to a depth of 4 in. in 22 upland prairies where little bluestem alone formed 88 to 98% of the vegetation. Annual precipitation at the three groups of stations—Anita, in western Iowa, and Lincoln and Nelson in southeastern Nebraska—was 32, 29, and 26 in., respectively. The yields of plant materials in these silt loam soils were, in the same order, 3.15, 2.60 and 2.34 T/A. (Fig. 5). Correlation between the average dry weight and the mean

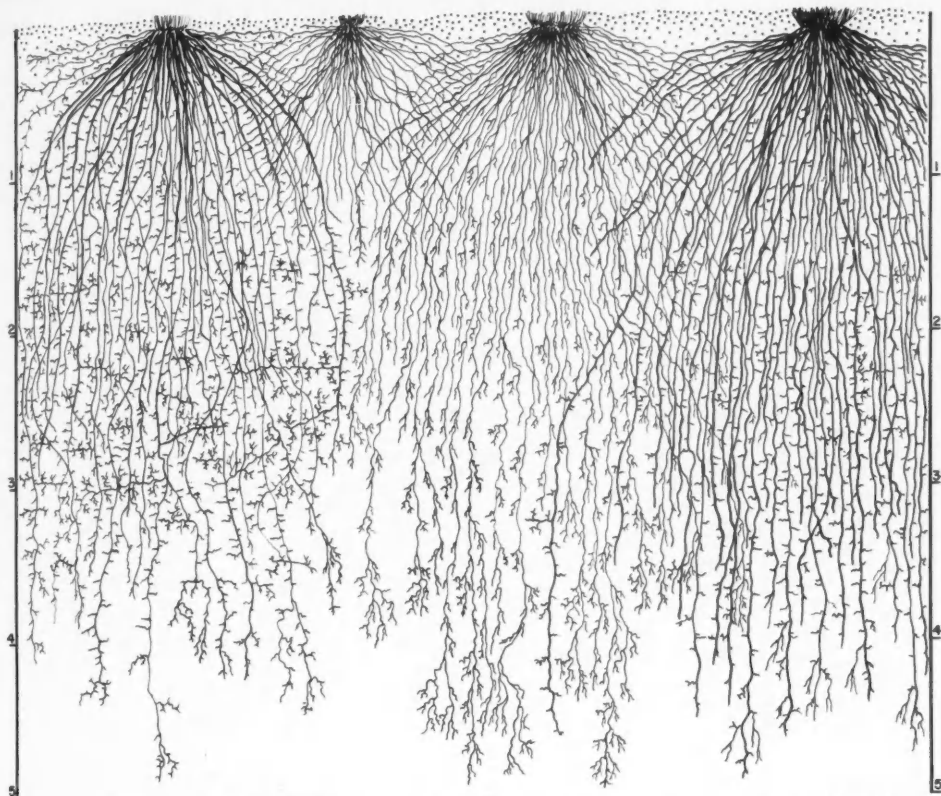


FIG. 4. Characteristic development of roots of 3 upland bunch grasses as they occur in the little bluestem community or in their own communities. From left to right are needlegrass (*Stipa spartea*), interstitial Junegrass (*Koeleria cristata*), little bluestem (*Andropogon scoparius*), and prairie dropseed (*Sporobolus heterolepis*). Average number of roots in the first inch of soil in the trench wall is shown except in the first 2 ft. Scale in feet, height of foliage by midsummer is 1.5-2.5 ft; flower stalks extend upward mostly 2.5-3.5 ft.

annual precipitation at each station was found to be very significant. Coefficient of correlation of the little bluestem was .642, of the big bluestem series, already described, .673. Volume of these materials was also determined. Statistical treatment of the data from each series showed that the correlation between volume and weight was very significant. Coefficients of correlation were .870 and .874, respectively (Shively & Weaver 1939).

These are samples of the furrow slice that the breaking plow clove neatly from the surface of the soil. The pioneer walked behind the plow in a clean, cool, moist path of richness. The furrow slice was a long, almost unbroken strand of turf, each one laid smoothly against the former one. A study of the binding network of roots showed that a single strip of Iowa prairie sod, 8 in. wide, 100 in. long, to a depth of 4 in. is bound together with a tangled network of roots having a total length of more than 20 mi (Pavlychenko 1942).

The average weight of roots occurring at 4-12 in. depth at Lincoln was one-third the total weight of

underground parts in the surface 4 in. (3.3 T) or 1.1 T/A. Root weight nearly always decreases rapidly with soil depth. That from a foot-wide monolith in silty clay loam decreased from 85.8% in the first 6 in. to 5.3 in the second, and then, foot by foot, from 5.0 to 2.3, 1.4 and 0.2%.

Stem bases and roots of bluestems constituted about 10% of the total organic matter in the upper 6 in. of soil. The amount decreased gradually to 3-4% in the second 6 in. to 1% in the fourth foot under little bluestem in an upland (Lancaster) soil. A similar gradual decrease under big bluestem in a lowland (Wabash) soil was ascertained to a depth of 7 ft. Below the surface 6 in. of soil in native grassland, there has been found an approximate linear relation between the amount of root material and the amount of soil organic matter in the various soil horizons (Weaver, Hougren & Weldon 1935). This indicates that organic materials had accumulated in larger quantities at those depths where the roots had been most concentrated. Extensive early studies by Alway & McDole (1916) have shown that in grassland soils



FIG. 5. (Upper) One-half sq m of underground parts of little bluestem (*Andropogon scoparius*) to a depth of 4 in. at Nelson, Nebraska, a drier type of true prairie as is shown by the pronounced bunch habit. (Lower) Part of a similar area of underground parts of needlegrass (*Stipa spartea*) to 4 in. depth at Lincoln. The sod mat is inverted.

the nitrogen and organic matter decrease regularly with depth, the bulk of the organic matter being confined to the surface foot (Russel & McRuer 1927).

NEEDLEGRASS

Stipa spartea often occurs intermixed with little bluestem but it is also a dominant of a second upland community. The bases of the widely spaced, usually circular bunches vary from 1-4.5 in. in diameter. Basal cover is only about two-thirds that of little bluestem. It averages only 11%. Foliage varies from 1.5-3 ft in height and flower stalks range from 2-4 ft.

The root system of mature plants usually reaches depths of about 4.5 but sometimes 6 ft. Numerous, profusely branched, smaller roots occupy the surface soil, spreading horizontally or mostly diagonally downward to a distance of 8-18 in. The longer roots give rise to many laterals which divide into fine branches in the deeper soil. Careful examination of the usual prismatic structure of the B horizon (subsoil) reveals patterns of root branching as indicated in Fig. 4.

The average weight of roots at 4-12 in. depth at Lincoln was 48% (0.89 T) of that of underground parts in the 0- to 4-in. level (1.87 T).

Total length of roots of needlegrass occurring in

the 0.5 sq m sample, partly shown in Fig. 5, was ascertained by Pavlychenko (1942) to exceed 11 mi.

PRAIRIE DROPSEED

Sporobolus heterolepis is another bunch grass of uplands which intermixes somewhat with little bluestem and needlegrass but also forms limited communities of its own. This warm-season grass produces circular bunches from less than 0.5 ft. to 1.5 ft in width. Foliage height is mostly 8-18 in. and flower stalks are 2.5-3 ft high. The root system is very similar to that of little bluestem, but the roots are coarser and branch somewhat more horizontally. Roots spread 1-2 ft in the upper soil but many extend vertically downward 4-5 ft (Fig. 4). The average dry weight of plant materials in the surface 4 in. is considerably greater than that of needlegrass, and also greater than that of little bluestem.

BIG BLUESTEM

Big bluestem occurs commonly on uplands. On lower and midslopes it not only shares dominance with little bluestem but also regularly forms 5-20% of the grass cover in the little bluestem type of uplands except on the drier hilltops and ridges. On upland it usually occurs in the bunch form and height is considerably reduced. Roots were 1-2 ft less in depth

than on lowland and some also spread outward in the upper soil. The main roots were usually much finer and better branched, and somewhat more of the root weight occurred near the surface of the soil. Root habits of this grass have been studied in ten soil types.

OTHER GRASSES

Side-oats grama (*Bouteloua curtipendula*) is a common but rather minor constituent of upland prairie. It is far more abundant in mixed prairie westward where its root habits will be described. The rather fine well-branched roots spread 1-1.5 ft laterally and attain depths of 4-5.5 ft.

Junegrass (*Koeleria cristata*) has a shallow but exceedingly well-developed root system. From the base of the small bunches some of these very fine roots, scarcely exceeding 0.2 mm in diameter but much branched, spread horizontally or obliquely to about 8 in. Others penetrate nearly vertically downward, but usually only 15-20 in. (Fig. 4). It is a drought evader, profiting by early growth, summer dormancy, and autumnal development. Its life span is shorter and it is less persistent than most grasses.

Penn sedge (*Carex pennsylvanica*) is a low-growing rhizomatous plant which absorbs chiefly in the first 2 ft of soil, but sometimes to 3 ft. Roots of Scribner's panic grass (*Panicum scribnerianum*), another low-growing species, spread widely throughout the surface 2-3.5 ft of soil.

Kentucky bluegrass (*Poa pratensis*), an introduced rhizomatous plant, has spread widely since the cessation of prairie fires and under the practice of annual mowing. It has a wonderfully well-developed root system. The fine, thickly branched, thread-like roots form dense mats especially in the surface 1.5 to 2 ft of soil. The longest are sometimes 3 ft deep.

Western wheatgrass (*Agropyron smithii*), sand dropseed (*Sporobolus cryptandrus*), blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) were species of minor importance before the 7-year drought. They are all dominants of mixed prairie for which the root systems will be described. The decrease in stature of lowland grasses (switchgrass, Canada wild-rye, and Indian grass) where they have migrated along ravines often halfway up the hills, is marked. This is accompanied by an increase in lateral spread of surface roots and the production of networks of branches.

Except for a few upland grasses and sedges, the diagram in Figure 4 mirrors faithfully the root habits in upland prairie communities.

EXPERIMENTS WITH UNDERGROUND PARTS

When one examines a diagram of the roots, as in Figure 4, he may wonder about the actual number in the surface soil, their tensile strength, and their effect on holding the soil in place. The number of main roots has been ascertained by Pavlychenko (1942) on representative samples of sod of several prairie grasses selected by the writer as representative of average conditions. In the upper 10 cm of soil they occurred

in decreasing numbers (to the nearest hundred per 0.5 sq m 5.38 sq ft): *Poa pratensis* 16,300; *Agropyron smithii* 11,500; *Bouteloua gracilis* 5,800; *Stipa spartea* and *Sporobolus cryptandrus* 4,400 each; *Andropogon gerardi* 3,500; and *A. scoparius* 3,400. He also ascertained that the tensile strength, expressed in grams, of the main roots of each species in the above order was 273, 849, 757, 981, 821, 1,712 and 1,171. Thus, the very fine roots of Kentucky bluegrass showed the least tensile strength and the coarse ones of big bluestem the greatest.

The main roots exert considerable binding effect upon the soil. But, as Pavlychenko (1942) points out, "their chief significance, however, rests in their ability to produce multitudes of branches. These penetrate the soil in all directions and come into contact with the smallest soil particles. Unlike main roots, they are composed largely of young, actively absorbing tissue." Their tensile strength has also been ascertained; in little bluestem, for example, it varied from 31 gm for branches of the first order to 2 gm for those of the third. Of all the underground parts of the preceding, rhizomes of little bluestem and roots of big bluestem exhibited the greatest tensile strength. Tensile strength is involved in resistance to frost heaving, especially of seedlings but its main value is that of resistance to soil erosion. Poorly anchored plants, but not those of native prairie, may be pulled up during grazing. The binding of soil by roots as well as the process of granulation continues under the action of long-lived and regularly renewed growth of roots of prairie grass.

The binding power of underground plant parts and their resistance to erosion have been ascertained by a series of experiments (Weaver & Harmon 1935). Similar soils without living roots or with only the roots of weeds, when placed under the same conditions of erosion, were washed away in only a small fraction of the time required to erode the prairie sod when the grasses were cut at the soil surface and removed. Even the best growth of field crops is far inferior to the native bluestems in preventing the soil from washing away (Kramer & Weaver 1936). Once the prairie was destroyed, the deep, thick topsoil (A horizon) of Iowa, protected for thousands of years by prairie sod, lost about one-third of its original depth during a single century under cultivation. Moreover, depletion of mineral nutrients is making necessary additions of fertilizers. Unlike prairie plants, cereal crops take more from the soil than they put back into it.

An examination of roots in Figure 4 indicates that there must be very great competition between plants for water and nutrients. This is entirely correct. As has been shown repeatedly, production of any prairie grass may be increased and often doubled simply by removing other grasses from a few feet on all sides of it (Clements, Weaver & Hanson 1929). These long-lived, perennial root systems may absorb water at all times except in winter when the soil is frozen, often to a depth of 8 to 18 in. Although some new roots are developed each year, it is believed that the

bulk of the root system undergoes very gradual change.

Although no studies on the activities of native grasses in fall and winter have been made, the number, length, and absorbing area of roots of winter wheat were ascertained at 10-day intervals during the fall and at longer intervals during winter and spring. The development of both roots and shoots fell into three rather distinct periods, temperature being the controlling factor (Weaver, Kramer & Reed 1924).

It has been shown experimentally that from early spring until the middle of May, soil with needlegrass loses 2 to 3 times as much water as that under the later-growing little bluestem (Weaver & Albertson 1943). During summer absorption by needlegrass is less than that of bluestem, but it increases again in autumn. Upland grasses depend entirely for their water supply upon precipitation. In a series of extensive studies approximately 200 samples of prairie sod were collected from 24 stations distributed over a region extending several hundred miles from east to west. More than 10 tons of soil were removed from prairies of Iowa, Nebraska, Kansas, and Colorado, and transported to Lincoln. A comparison of the yields of 67 samples from upland in true and mixed prairie in relation to precipitation is of special interest. The mixed prairie stations were from Hays, Kansas, northward to Holdrege, Nebraska (Fig. 3). Mean annual precipitation at the Anita, Lincoln, Nelson and Holdrege station groups was 32, 29, 26 and 23 in., respectively. If weights of the Anita group are considered as 100%, those from the other stations were 80, 73, and 64%, respectively. Here again there was a close correlation between yield of underground parts and precipitation.

The rate of production of the large quantities of roots of little bluestem has been ascertained. Plants were grown from seedlings to maturity under conditions described for big bluestem. The first year it produced 56% of its mature weight, which it attained at the end of the second summer; the underground materials produced were similar in amounts to those found in typical mature stands in native prairie.

Although blue grama is far more abundant in mixed prairie, its rate of production underground was also ascertained with these studies on the bluestems at Lincoln. It reached its maximum development the second growing season, producing 64% of this weight the first summer. With both little bluestem and blue grama, yields of the controls allowed to grow a third year did not exceed the weight attained the second summer.

The weights of roots alone (minus stem bases and rhizomes) produced in these experiments amounted to approximately 5.5 T/A in big bluestem, 2.7 in little bluestem, and 1.6 in blue grama. These amounts might be expected after 3 years' growth of full stands of similar grasses cut annually for hay (Weaver & Zink 1946).

Roots of little bluestem and blue grama were among the 3,400 roots of young plants banded to determine

their length of life. After 2 years about 66% of the banded roots were alive. By the autumn of the third year the number had decreased to 10 and 45%, respectively, for the two species. These losses were almost negligible, since the total number of roots per plant was now very large (Weaver & Zink 1946a).

Rate of decay of roots and rhizomes of little bluestem and western wheatgrass left in the soil when the grasses were killed was similar to that of big bluestem. A period of 3 or 4 yrs was required for complete disintegration. The most resistant to decay were blue grama, side-oats grama, and buffalo grass. Here much undecayed material remained and some roots of each species retained moderate tensile strength after 3 yrs. It is of interest that roots of Sudan grass and smooth brome grown for one summer disintegrated as far in 1 yr as did many perennial native grasses in 3 yrs (Weaver 1947).

DISCUSSION AND INTERPRETATION

In upland prairie differences in soil horizons are more pronounced and exert greater effects upon root distribution than those of lowland. As a result of the processes of development, the mellow surface 16-18 in. of soil has a granular structure. Much of the colloidal clay has been eluviated into the B horizon. This granular structure has resulted from alternate wetting and drying, repeated freezing and thawing, a high humus content and the favorable effects of root activities. Roots penetrate this granular layer easily, they spread widely and branch repeatedly. This rich layer has the greatest number of roots, and they can be separated from the soil with little difficulty.

In the subsoil or B horizon the clay content is higher and much of the lime has been leached. Here the soil often has a prismatic structure. The vertical prisms are often 2-3 in. in diameter and 8-12 in. in length, with vertical cracks between them when the clay shrinks in drought. Penetration of roots is much more difficult and branching is often less pronounced in the prismatic layer of soil. Here the rootlets are mostly appressed to the surfaces of the prisms where penetration is easy, water enters more readily, aeration is best, and nutrients apparently more concentrated. Fewer roots penetrate through the prisms. Roots of grasses are removed from this horizon, which is usually 1.5-3 ft deep, with much more difficulty than from the granular layer above or the massive layer below, where there is less clay. Lime occurs in amounts sufficient to give the parent materials a mellow structure. In Figure 4 the effects of the B horizon upon the branching of roots of needlegrass are indicated. Other effects of soil structure on roots will be shown elsewhere.

The finer and much more branched roots of plants of upland seem better adapted to penetrate and absorb water and nutrients from the drier and more compact soil than the coarser roots of the tall grasses of lowlands.

In the deep fertile soils of the prairie, with its favorable climate for the growth of grasses, water con-

tent of soil and rate of water loss influence root development of underground parts perhaps more than any other environmental condition. Precipitation varies from about 23 in. in the west-central portion to about 33 on the eastern border of the area under consideration. Nearly 80% falls during the growing season and long periods of severe drought are not common.

Alway, McDole & Trumbull (1919) found the surface 2-3 ft of upland prairie at Lincoln dried to near the point of unavailable moisture on only three occasions in the 6 yrs, 1906 to 1912. From 1909 to 1912 the moisture content of the first foot of the prairie soil was reduced to the hygroscopic coefficient only once.

Results of a 13-year study of soil moisture in upland (1916-1928) have already been presented in comparison with that on lowland.

Available soil moisture was ascertained at 3 groups of stations (3 widely distributed prairies in each) during the dry year (1940), which was the last year of the 1933-40 drought, and the moderately wet year, 1941. In 1940, at the western Iowa stations, rainfall was sufficient to keep the soil continuously moist to a depth of 6 ft, except for a moderate midsummer drought. In the drought-damaged bluestem prairies of eastern Nebraska, severe drought began in midsummer and available soil moisture was exhausted to a depth of 5 ft. In the mixed prairie on the High Plains of western Kansas, where the cover of vegetation had been reduced to about 10% normal, drought began in May. Usually the surface foot of soil alone had available water, but only temporarily and at widely separated intervals.

In 1941 in Iowa, water content was available for growth to a depth of 6 ft, at least until August. There was moderate drought in late summer at one station. In eastern Nebraska prairies both rainfall and soil moisture were less, but the general pattern of water distribution was the same. In the soil of the western Kansas stations, an excellent supply of available soil moisture usually prevailed. These data are illustrative of water content of soil which has been determined regularly in both true prairie and mixed prairie over a long period of years.

Extreme environmental conditions to which prairie vegetation near Lincoln was subjected in midsummer, 1943, and from which it has recovered were as follows. The average daily maximum temperature increased week by week from 88° to 111°F, and average day temperatures ranged upward from 77° to over 100°. The average daily minimum humidity over a period of 6 weeks did not exceed 22% and it was as low as 15%. Minimum humidity of 3-5% was recorded on some afternoons. The rate of evaporation was often twice and sometimes nearly 3 times as great as that recorded in prairie during the 3 preceding years. Water for growth became unavailable to 3 ft in depth in July and to 4 ft in August, and less than 2% water was available in the fifth and sixth foot (Weaver, Stodart & Noll 1935).

During the years of great drought (1933-40) it was

repeatedly observed that death of plants was directly correlated with depth of the root systems. The first to succumb were the more shallowly rooted plants. In true prairie these were Junegrass, Kentucky bluegrass and Scribner's panic grass. On uplands big bluestem persisted in small amounts where little bluestem died. Death resulted when no available water occurred to a depth of about 4 ft. Through its deeper roots big bluestem continued to absorb enough moisture from 1-2 ft of moist soil below this level to maintain life.

On the Great Plains marked changes in root habits resulted from drought. Roots of blue grama and buffalo grass were profoundly reduced in numbers, spread, and depth of penetration. Often only 10% or less of the former number occurred in the upper soil, lateral spread was usually not more than a third normal, and living roots were usually confined to the first 8-12 in. of soil. The reaction of each of the most important grasses of both prairie and plains to severe drought has been described (Weaver & Albertson 1943).

During the last years of the great drought of the 30's current rainfall in true prairie moistened only the upper 2-2.5 ft of soil. Below, a dry layer of soil with no water available for growth extended downward to as much as 5.5 ft. This condition was common over most upland, eastern Nebraska prairies. In areas badly denuded by drought, much soil between the widely spaced relics was almost free from living roots. Depths of roots of invading western wheatgrass, sand dropseed and big bluestem were confined by the dry layer to the upper 2-2.5 ft of soil. During the following years of heavy rainfall when the soil was again moistened deeply, the grass roots extended to their usual depths.

Growth of vegetation begins slowly in April, when the cool-season grasses and sedges resume activity. Early in June they attain a foliage height of 1-2 ft. Flower stalks of needlegrass and western wheatgrass may add 8-18 in. to this height. Early in May little bluestem attains a height of 3-4 in. and late in July about 1.5 ft. Flower stalks then elongate rapidly and reach a height of 2-2.5 ft. The average percentage of little bluestem by weight during 3 yrs was 2% in April, 26 in May, 36 in June, and 21 in July. The 13% increase of weight in August and 2% in September consisted almost entirely of flower stalk production (Flory 1936). Development of other warm-season grasses—prairie dropseed, big bluestem and side-oats grama—is very much the same. These warm-season grasses overwhelmingly predominate. Thus, the cover of grasses, as on lowland, develops steadily in summer and fruition extends into autumn. This cover differs from that of lowlands in that it is composed almost entirely of bunch grasses, it is a little less than one-third as high, and the yearly production of forage is only about half as great.

Since the bunches and tufts of grasses are spaced several inches distant, a lateral spreading from the base of the clump into the soil below these interspaces would be expected. Moreover, the great demands for

water from this rich, deep but somewhat drier subsoil promotes deep rooting and extensive branching. Just as the coarsest and most poorly branched roots of grasses occur in moist to wet lowlands and the finest and most extensively branched ones occur in dry mixed prairie (as will be shown), in these less xeric upland prairies an intermediate condition prevails.

The soil (solum) is somewhat shallower than on lowlands and it depends entirely upon precipitation for its renewable water supply since the water table is far beyond the depths of the longest roots.

Experiments extending over a period of several years on upland prairies near Lincoln have shown that average daily water losses during the growing season ranged from 19 to 32 T/A (Flory 1936, Fredricksen 1938). Thus, the soil reservoir is more or less depleted of water and made ready to absorb the precipitation from subsequent showers. The frequently low soil moisture content of late summer and fall results in part from the luxuriant growth of the plant cover and an enormous expenditure of water, and only partly from a lack of rainfall.

UNDERGROUND PARTS OF GRASSES OF MIXED PRAIRIE OF HARD LANDS

Over the vast extent of mixed prairie, a large number of grasses of great abundance occur. Hence the communities are more numerous than in true prairie. They have recently been described by Weaver & Albertson (1956). Only a few of the grasses of great abundance in true prairie extend far westward over the Great Plains. Most mixed prairie grasses are of a more xeric kind. In general, tall grasses are not found except on sandy soil and sand hills, and they are different species from those of lowland true prairie. They will be considered separately.

As precipitation decreases and evaporation increases westward, the vegetation becomes sparser and less luxuriant, soils become lighter in color and decrease in depth. West of the Chernozems, Dark Brown Soils and Brown Soils have developed. Vegetation on the Dark Brown Soils while not luxuriant is still well-developed, especially the underground parts. The zone of lime accumulation decreases in depth compared with that in Chernozem. The B horizon, with less humus, is lighter brown and contains the calcium accumulations. The lime zone becomes still shallower in the Brown Soils where it may occur at 8-12 in. depths. This zone varies from a few to 18 in. or more in thickness. When it is moist, roots easily penetrate through it. The fertile Dark Brown Soils and the best Brown Soils are used for wheat production, despite the hazardous climate. Grazing predominates over the more rolling terrain of the area of Brown Soils.

Organic matter decreases gradually westward as follows: Anita Iowa stations 7.1%, Lincoln stations 6.1, Nelson stations 5.4, Phillipsburg stations 4.4, and Burlington stations 2.7%. Soil nitrogen decreases similarly from .308%, .271, .248, .198 to .130%. These decreases occurring under approximately the

same mean annual temperature (48.6-50.2° F.) are due partly to the smaller amount of vegetation from which organic matter is formed and partly because it is more rapidly oxidized, both the result of an increasingly more arid climate (Shively & Weaver 1939).

The greater percentage of Plains' soils consist of clay loams, silt loams, and sandy loams, often referred to in the literature as "hard lands," which, of course, they are not, in contrast to the sandy soils ("soft lands") which have little or no cohesive properties. However, hard lands, when dry, become very compact and often a pick is necessary to remove the soil. These soils are frequently moist to a depth of several feet; the water below 12-18 in. is not removed by evaporation but only by absorption through plant roots.

Over the Great Plains wind movement is more frequent and much greater than eastward, humidity is relatively low, day temperatures and evaporation are high, and periods of summer drought are frequent. Nutrients have not been leached from the soil and plant growth is controlled largely by available soil water.

Transition from true to mixed prairie occurs gradually over an ecotone about 50 mi in width at 98°30' W longitude (Weaver & Bruner 1954). Mixed prairie is limited on the east by soil moisture from 25 in. or more of precipitation. This is sufficient to support a continuous growth of mid-grasses under which a short-grass understory is kept out by the dense shade. Rainfall decreases to about 15 in. near the mountain border, about 400 mi westward.

Important changes from true to mixed prairie are reduction in height and volume of vegetation without decrease in average root depth. Changes in the plant cover are from more mesic to distinctly more xeric species. Sod-forming species become common in the understory; among mid grasses the bunch habit prevails. In drought and cold their foliage cures on the stems and retains its value for forage.

The term short grass applies to grasses and sedges only 5-18 in. tall, such as blue grama, hairy grama (*Bouteloua hirsuta*), buffalo grass, and thread-leaf sedge (*Carex filifolia*). Moreover, it applies only to the plant parts above ground, since short grasses usually root as deeply as mid grasses. It is important to note that both have an equal opportunity to absorb water and nutrients at the several soil depths.

BUFFALO GRASS

Buchloe dactyloides is a warm-season, sod-forming grass with foliage 4-5 in. high and flower stalks 4-8 in. tall. Roots are much finer than those of most plains grasses. They are less than 1 mm in diameter but tough and wiry. They are very numerous and occupy the soil thoroughly. Many spread almost horizontally 6 to more than 18 in. in the surface 6 in. The bulk of the main roots pursue an almost vertically downward course to depths of 4-6 ft. Very fine thread-like branches occur in great abundance (Fig. 6). Roots have been examined in many soil types in

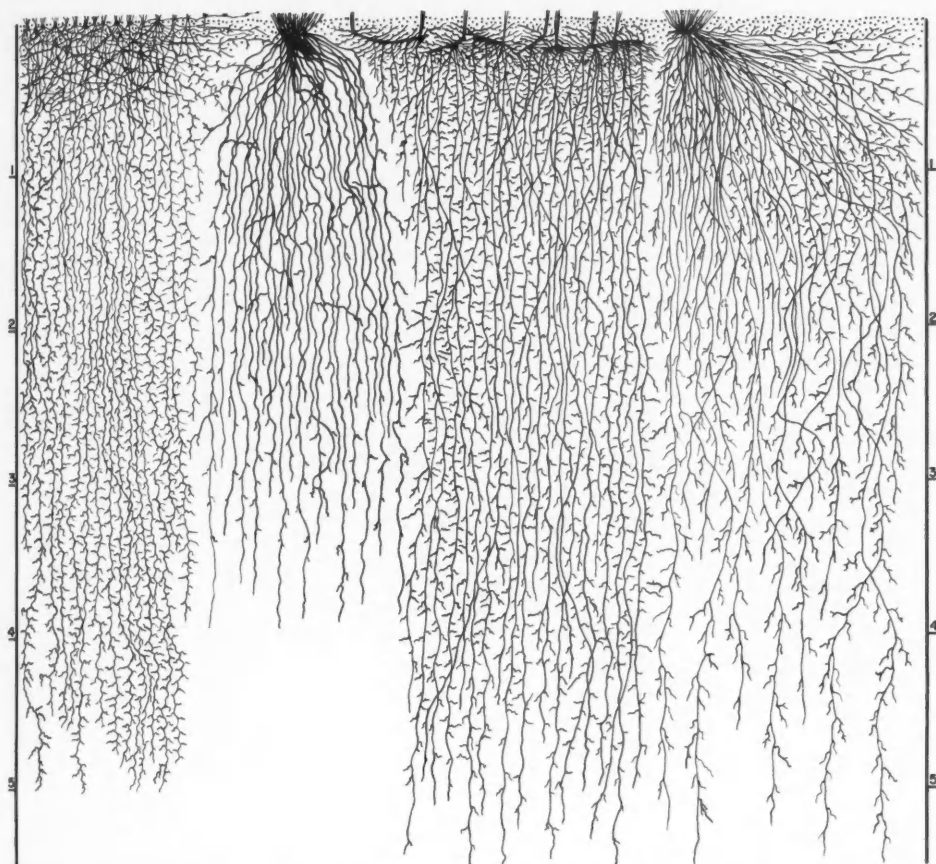


FIG. 6. Representative root systems of dominant grasses of mixed prairie communities as they occur in an in-thick layer of soil in a trench wall. From left to right are buffalo grass (*Buchloë dactyloides*), purple three-awn (*Aristida purpurea*), western wheatgrass (*Agropyron smithii*), and side oats grama (*Bouteloua curtipendula*). The average number of roots is shown throughout, except the fine ones of western wheatgrass in the surface soil. Scale in feet. Height of foliage ranges from 4-18 in. and flower stalks are usually 5 in. to 2.5 ft. tall.

the hard lands of the Great Plains at widely separated stations.

Sod produced by buffalo grass is dense, tough, and resistant to erosion. When cut a few inches deep into strips 12-15 in. wide, it can be rolled in the manner of bluegrass sod.

The root system developed so rapidly that seedlings presented a network of roots in the first 2 ft of soil at the end of the first summer and some roots were a foot deeper. The efficiency of the primary root alone is remarkable. A single seedling in 2 months tillered profusely, produced a leafy stolon 5 in. long and 137 leaves with a total area of approximately 20 sq in. Water and nutrients were absorbed by a hair-like seminal root, the others being constantly removed (Weaver & Zink 1945).

Root distribution to 4 ft in Holdrege silt loam on upland and a Chernozem Wabash silt loam of lowland was very similar. Approximately 70% by weight

occurred in the first 6 in. and 11.5% in the second. Then foot by foot at increasing depths it was 11, 4, and 3%.

BLUE GRAMA

Bouteloua gracilis is the most drought resistant of all the plains grasses in the Nebraska-Kansas-Colorado region (Mueller & Weaver 1942; Weaver & Albertson 1943). Like buffalo grass it has small leaves which develop near the soil surface. Foliage height is 3-5 in. and flower stalks are 8-14 in. high. The tufts are closely grouped and a basal cover of 60-80% is attained in good stands. Roots of blue grama are so similar to those of buffalo grass that they are almost indistinguishable. The wonderfully developed network of shallow roots and their spreading habit are the same. Thus, the bare places between the mats of both blue grama and buffalo grass, which are of usual occurrence, are normally as well occupied by roots as the soil beneath the plants. Both plants are thus



FIG. 7. (Upper) Underground parts of an excellent stand of blue grama (*Bouteloua gracilis*) in .5 sq m of surface soil in mixed prairie at Phillipsburg, Kansas. (Lower) Invasion of western wheatgrass into big bluestem sod. The soil was washed away from this .5 sq m area, revealing the dead underground parts of the former dominant (black) and the shining white rhizomes of wheatgrass at Belleville, Kansas.

able to benefit from water furnished by light showers. Under the increased precipitation of true prairie eastward, this wide spreading of lateral roots rarely occurred. At the many stations in mixed prairie where root depth was ascertained, it ranged between 4-6 ft.

A comparison was made of 36 samples of (0.5 sq m) of underground parts to 4 in. depth. They were taken at groups of stations from Lincoln to Colorado Springs. No consistent differences in dry weights of either blue grama or buffalo grass in the several areas were found. Yields averaged about 2 T/A. The almost continuous network of stem bases and fine roots in the first 4 in. of soil under a good stand of blue grama is shown in Figure 7.

From monolith samples of blue grama in mixed prairie, it was ascertained that about 79% of the weight of underground parts occurred in the first 6 in. of soil and 10% in the second 6-in. layer. The second foot yielded 7%, the third about 3% and the fourth only 1%.

PURPLE THREE-AWN

Aristida purpurea, a bunch grass 12-20 in. tall, has somewhat coarser roots than blue grama. Some extend outward 5-8 in. before turning downward; others

grow directly downward to depths of 4 ft and some to 5 ft. There was little branching in the surface 4 in. of soil. Usually the root system lacks the abundant laterals so pronounced on short grasses. This grass is also less drought resistant than buffalo grass and blue grama (Fig. 6).

WESTERN WHEATGRASS

Agropyron smithii is one of the few sod-forming species. This cool-season grass is 2-3 ft tall in good years, but is much dwarfed by drought. The extensive, much branched, tough rhizomes are 1-2 mm thick. They occur within a few inches of the soil surface. From these and the bases of the plants many roots run out somewhat horizontally in the surface 12-18 in. of soil (Fig. 6). They are profoundly branched to the third and fourth order and thus furnish an excellent surface absorbing system. Other roots extend obliquely and still others almost directly downward. Depth of penetration varies with soil from 5-7 ft. The roots are branched throughout.

Roots were examined in many places in 4 states. The chief differences in the root habit of this grass in both upland and lowland true prairie, as compared with mixed prairie, were the lack of an extensive

surface absorbing system and the greater depth of penetration (8-9 ft).

Extensive studies in true prairie of eastern South Dakota, Nebraska and Kansas have shown that wheatgrass composed scarcely any part of this grassland. Only the great losses sustained by the bluestems and the bare areas thus produced made possible the remarkable spread of wheatgrass (Fig. 7). But in mixed prairie it has always been widely spread, and with an understory of short grasses, chiefly buffalo grass, it dominates wide areas, especially on heavy compacted soil. The vitality of the rhizomes and their resistance to drought is remarkable (Mueller 1941).

The amount of underground parts of wheatgrass in the surface 4 in. of soil at mixed prairie stations near Burlington, Colorado, was 2-2.2 T/A.

Weight of underground parts in the surface 6 in. averaged 55% of the total. The second 6 in. yielded 15% and the second foot 16%. The remainder was in the deeper soil. Thus, the root-weight of this drought-evading grass is more deeply placed than that of most other species.

SIDE-OATS GRAMA

Bouteloua curtipendula is a very drought resistant, warm-season, mid grass. It usually occurs in small to wide bunches and attains a height varying from 1.5 to more than 2 ft. Roots are not so fine as those of buffalo grass or blue grama, but about 1 mm in diameter. Many roots spread outward 1-1.5 ft in the surface 2-4 in. of soil. Others run obliquely or nearly vertically downward. All are extremely well branched, mostly with rootlets 1-3 in. long. Depths of penetration of 4.5 to 5.5 ft were attained (Fig. 6).

NEEDLE-AND-THREAD

Stipa comata is a cool-season grass which occurs on both hard land and sand. The bunches are small, usually only 1-3 in. in diameter, and not closely spaced. Plants vary in height from 1-3 ft. This grass has a widely spreading, deep, and exceedingly well-branched root system. The main roots are about 1 mm in diameter. Many have a lateral spread of 14 in. in the surface 6 in. of soil and 18 in. in the first foot. To a depth of 2.5 ft the main roots are only a few mm apart and the interspaces are well filled with horizontal, well branched rootlets. Many roots extend into the fourth and fifth foot of soil.

OTHER GRASSES

Thread-leaf sedge (*Carex filifolia*) is grass-like in appearance and habit. It grows in dense bunches 4-6 in. in width and has about the same stature as blue grama. The tough, black, wiry roots bind the soil more firmly than most grasses. They are a mm or less in diameter but occur in enormous numbers. They seldom descend vertically but run obliquely away from, as well as under, the plant to distances of 2-2.5 ft. They are profusely branched and end in brush-like mats. Many roots crisscross at various angles and reach depths of 4 ft. A few are 5 ft deep.

Green needlegrass (*Stipa viridula*), a bunch former 1.5-3 ft high, has a root system very similar to that of needle-and-thread.

The soil beneath bunches of sand dropseed (*Sporobolus cryptandrus*) and at least 12 in. on all sides is filled with a vast network of small roots and masses of finely-branched rootlets to a depth of 3-4 ft. Some roots extend even deeper. This mid grass attains a height of 1.5-2.5 ft.

The widely distributed Junegrass has been described. In mixed prairie the plants are shorter and the bunches small. But the widely-spreading, rather shallow root system changes but little, except to branch more profusely in the surface soil.

Roots of ringgrass (*Muhlenbergia torreyi*) occupy the soil to depths of about 4 ft. Galleta (*Hilaria jamesii*), a xeric, sod-forming grass, also has a root depth of about 4 ft.

Thus, each of the dozen grasses described (except Junegrass) fits well into the diagram representing Great Plains grasses. All attained root depths of at least 4 ft in the many soil types in which they were examined.

OTHER STUDIES IN HARD LANDS

Root systems of a large number of grasses in 3 communities at Hays, Kansas, have been described by Albertson (1937). Soil profiles and root depths in each community are given. In the short-grass (blue grama and buffalo grass) type of the drier uplands, grasses with foliage heights of 3-5 in. were rooted 4-5 ft deep. In the little bluestem community of moist, rocky hillsides, where the foliage of little bluestem was 8-16 in. tall, the grasses were rooted 3-5 ft deep. Heights of 2-3 ft were attained by mature tall grasses growing on lower slopes and in ravines, which received runoff water. Root depths of 5-6 ft were attained by big bluestem, switchgrass and western wheatgrass.

Extensive, earlier studies have been made by Shantz (1911) in the hard lands, sandy loam soils, and sand of eastern Colorado. He studied the natural vegetation as an indicator of the capabilities of land for crop production.

DISCUSSION AND INTERPRETATION

A comparison of the amount and time of available soil moisture in the Great Plains with that in true prairie and factors contributing to a drier atmosphere will aid in understanding the greater xerophytism of plants of mixed prairie and their root relations in shallower and drier soil.

Altitude increases from about 1,500 ft on the Plains eastern border to about 5,500 ft near the mountains in Colorado. This shortens the growing season a few weeks. Nights are cool but days are hot. Soil temperatures at Colorado Springs (June 5 to August 5) showed extreme variations in the 24-hr period from 60° or 70° F to 90° or 95° or even more at 4 in. depth. Not infrequently the surface soil (0.5 in. depth) ranged from 55°-60° F in early morning to 120°-125° in the afternoon. Relatively greater inso-

lation, resulting from a sparser cover of vegetation to absorb radiant energy, and an average lower specific heat of the drier soil combine to increase the day soil temperatures greatly over those of true prairie. However, it seems quite certain that water content of soil and air, and not temperature, is by far the most important factor in root development.

The fine textured soils have a high water-holding capacity. Considerable moisture is held from late fall, winter, and early spring before transpiration losses from vegetation become great. Absorption of rain falling in short, heavy showers is relatively inefficient both because of high runoff and great loss by evaporation. When the supply of stored moisture is exhausted vegetation undergoes long periods of summer drought.

Water content of soil in prairie and plains, with other environmental factors, was ascertained at Lincoln, Nebraska, and in mixed prairie at Phillipsburg, Kansas, and Burlington, Colorado, during 3 years of rather normal precipitation. Rainfall is 5 in. less at Phillipsburg and 11 in. less at Burlington than the 28 in. at Lincoln.

In 1920, at Lincoln, a sufficient amount of water to promote good growth was available at all depths at all times. At Phillipsburg, July and early August were periods of drought and at times, of actual water deficiency. Available water supply was favorable at Burlington until June, but after this time marked deficiencies were of frequent occurrence.

In 1921 at least 5 and usually 8-10% available water existed at all times to depths of 4 ft at Lincoln. At Phillipsburg the nonavailable point was approached once in July and twice in August; no water was available to a depth of 4 ft in late summer. At Burlington no water was available at any time for growth in the third and fourth foot of soil, and after June 30 it was depleted repeatedly in the first and second foot.

In 1922 the season was fairly favorable for growth, except the latter part, when severe drought occurred at all stations, though it was relatively less marked at Burlington. A margin of 5-11% available water existed at all times to a depth of 4 ft at Lincoln. At Phillipsburg drought began late in June and continued throughout the summer. There was often no water available to a depth of 4 ft at Burlington. The soil in spring and early summer was, as usual, quite moist, but deficiencies were marked and almost continuous after the middle of June.¹

The value of water content to the plant, however, is not determined entirely by its quantity but also by the rate of loss both through the plant and by surface evaporation. These in turn are controlled by humidity as affected by temperature, wind, etc., all of which are more or less integrated in evaporation. Evaporation was lowest at Lincoln and highest at Burlington, where it was 2-2.5 times as great. During the 3 growing seasons, conditions for plant growth in respect to rainfall, soil water, temperature, humidity,

¹ Physical and chemical analyses of these soils and tables of water content may be found in "Experimental Vegetation" (Clements & Weaver 1924).

wind, and evaporation were most favorable at Lincoln, intermediate at Phillipsburg, and least favorable at Burlington.

The weekly record of available soil moisture to 5 ft in depth in mixed prairie at Hays, Kansas, extends (except for 1 yr) from 1935 to 1954, inclusive (Weaver & Albertson 1956). Also some earlier determinations are available (Albertson 1937; Weaver 1919).

The combined differences of lower rainfall, drier soil, greater evaporation, and less favorable temperatures for growth in mixed prairie are reflected both in the vegetational cover and root habit.

In mixed prairie, it was early ascertained that water relations of soil and air were controlling in plant development, other factors being merely contributory (Weaver 1924; Clements & Weaver 1924). For example, root development of winter wheat in the fertile silt loam soils in 20 fields from true prairie throughout western Kansas and eastern Colorado was ascertained. Average depth of roots was 5.3 ft and average lateral spread in the surface soil was 6 in. under a precipitation of 26-32 in. They were 4.2 ft and 9 in. under 21-24 in. of rain, and 2.3 ft and 12 in. in Colorado where precipitation was 16-19 in. Tops were proportionately smaller. Similar results were obtained with a variety of grass crops grown experimentally at Lincoln, Phillipsburg and Burlington (Weaver 1920).

The greatly increased branching habit of the shorter but more widely spreading roots in dry land is readily produced experimentally. For example, corn, with similar hereditary characters, was grown in moist, rich, loess soil with an available water content of 19 and 9%, respectively. After 5 weeks the first lot had a total root area 1.2 times greater than that of leaves and stems. Root area in the drier soil was 2.1 times greater than the tops. In the more moist soil primary branches furnished only 38% of the total root area, but 75% in the drier soil. Thus, a low water content, within certain limits, stimulates increased root branching (cf. Jean & Weaver 1924).

All of the Great Plains grasses are notably successful under the semiarid environment. The numerous cool-season grasses—needle-and-thread, western wheatgrass, Junegrass, thread-leaf sedge and others—begin growth early with the spring rains but may become semidormant in dry midsummer and thus evade the drought. They renew growth in autumn. The three grama grasses and buffalo grass are warm-season plants but they are extremely drought resistant. They endure long periods of dormancy, renew growth when rains come, and produce seed in early summer, late summer, or in fall.

This greater ability to cope with drought was revealed on a magnificent scale during the 1930's when grasses of true prairie were so sorely depleted. Not only the short grasses but also side-oats grama, western wheatgrass and sand dropseed spread over the drought-bared areas and flourished on the scanty precipitation during the drought years.

Volume of vegetation in mixed prairie is much less than that of true prairie and by weight annual forage production is normally half and often far less than

half as great. The grasses are wonderfully adapted to benefit from light rains. Water is absorbed at all soil levels and used as soon as possible for forage production. Root development in proportion to that of tops is greatly increased over that of true prairie. Root extent of short grasses and sedges is 4-16 times as great as plant height. That of mid grasses is 2-4 times as great. This grassland flora can adapt itself to dry cycles as well as to moist ones, a property not possessed by the plant cover substituted by agriculture.

UNDERGROUND PARTS OF GRASSES OF MIXED PRAIRIE OF LOESS HILLS

One physiographic section of the Great Plains is known as the Loess Hills. It must be given special attention for here the vegetation, although not different from that of the hard lands, is much more deeply rooted.

An area of loess hills several thousand square miles in extent lies southeast of the Nebraska sand hills and some loess hills extend southwestward near Holdrege, Nebraska, and Atwood, Kansas. Extensive studies of the origin of this loess by Lugn (1935) and Condra, Reed & Gordon (1947), have been summarized by Reed for the writer (Weaver & Bruner 1948). These loess depositions correlate with interglacial time; and wind, correlated with other factors, was the major force in the genesis of this loess.

The soils have developed from loess. Both soil and parent material to great depths are mellow and easily penetrable to both water and roots. Well developed soils of the upland are predominately of the Holdrege series, but over parts of the area the immature, light-colored Colby soils occur. They are approximately neutral in reaction. Both soils are very fine-textured. The degree of aggregation is very low. Organic matter is about 4-5% in the surface foot, and nitrogen 0.11-0.19%. The friable, dark-grayish-brown silt loam (A horizon) is about 12 in. deep in the Holdrege type. The subsoil (B horizon) of silty clay loam extends to a depth of 3 ft or more. The lime layer of this Chernozem occurs often between 3-6 ft in depth.

Mean annual precipitation is 23-24 in., nearly 80% occurring between April 1 and September 30. In May and June, drought is uncommon, distribution of rainfall in July is less favorable, and during August and September long periods of drought often occur. These are the conditions of soil and water supply for root development.

Depths of penetration of roots were reported by Weaver & Bruner (1948) as follows: buffalo grass 6.3 ft, blue grama 7, big bluestem 7.5, and western wheatgrass 10.3 ft, all from upland soils. Hopkins (1951) found that blue grama reached depths of 6.5 ft, little bluestem 8, side-oats grama 8, and big bluestem 10 ft. Even Junegrass added a foot to its usual root depth, extending downward to 2.5 ft. A somewhat similar increase in depth of various forbs was also noted; several species had root depths of 21 ft. Tomanek & Albertson (1957), working in loess hills

at Atwood in northwestern Kansas, noted very similar or even greater depths of root penetration.

The great depth of rooting in loess may be attributed to both physical and chemical conditions of the substratum. Water penetration is greater than on hard land. The percentage of readily soluble phosphorus in the organic matter is unusually high and may be a factor in promoting deep root growth. Effect of phosphates in promoting root growth in length and number of branches has long been known.

UNDERGROUND PARTS OF GRASSES OF SAND HILLS

Many areas with sandy soil or sand hills occur in every state in the Great Plains. The largest lies in central Nebraska where wind-blown, sand-hill topography extends over more than 18,000 sq mi. Some hills reach a height of more than 150 ft. Mixed prairie vegetation on sand is subjected to the same aerial environment as that of surrounding hard lands. Wind is one of the most important environmental factors of sandhill vegetation through its effect on shifting the sand. Geological evidence reveals that sand habitats have existed in this region since early Tertiary times.

Because of wind erosion, little soil development has occurred. The hills are composed mostly of fine-grained sand of a light-yellow color. The sand on the tops of dunes has a coarser texture than that on the sides and adjacent dry meadows. This is the result of the selective action of wind erosion. The finer sands contain sufficient silt to give them a light-gray color. Very little organic matter occurs in dune sands, but in the more stabilized dry meadows at their base small quantities of humus are present in the surface soils, which are classified under the Valentine soil series. Hygroscopic coefficients are 0.7-1.3% except the harder Valentine soils where they range from 3-3.5%.

Vegetation on sand presents several communities from blowouts and drifting sand to well stabilized grassland. Plants grow thickly only in the valleys. Vegetation is sparse on the hillsides and very thinly spread on the hilltops. "Communities characteristic of the true prairie (in its western extension) dominate the upper portions of the wet meadows and form a narrow zone of transition between the mesophytic, tallgrass communities at slightly lower levels and the less mesophytic, tall grasses of the dunes" (Tolstead 1942). Special attention will be given to the dominant grasses of stabilized climax communities. Many species are found only on sand, and those also common to hard lands often have modified root habits in sand.

Extensive studies have been made in the several communities and at various stations with rainfall varying from 15 to 20 in. or more. The earliest examination, 40 mi southeast of Colorado Springs, Colorado, was made in poorly vegetated, low sand hills. Mean annual precipitation was 15 in. but in some dry years it was only 8 in. This study revealed much shallower root development than that of similar plants in stabilized vegetation at Yuma, Colorado, Valentine, Haigler, Seneca, and Central City, all in Nebraska

where mean annual rainfall varied from about 17-26 in. (Fig. 3).

SAND BLUESTEM

The 3 most abundant tall grasses are sand bluestem, (*Andropogon hallii*), sand reed (*Calamovilfa longifolia*) and blowout grass (*Redfieldia flexuosa*). All are equipped with strong, extensive rhizomes. Sand bluestem forms loose open bunches with only a few coarse stems in each bunch. Thus, the basal cover is always small. The stems reach heights of 3-5 ft when flowering occurs after midsummer. The rhizomes, 4-9 in. long, elongate in spring and produce new stems and roots while the older rhizomes and roots slowly decay. Thus, there is a constant, if slow, migration. The outward spreading of the roots and the method of branching is shown in Fig. 8.

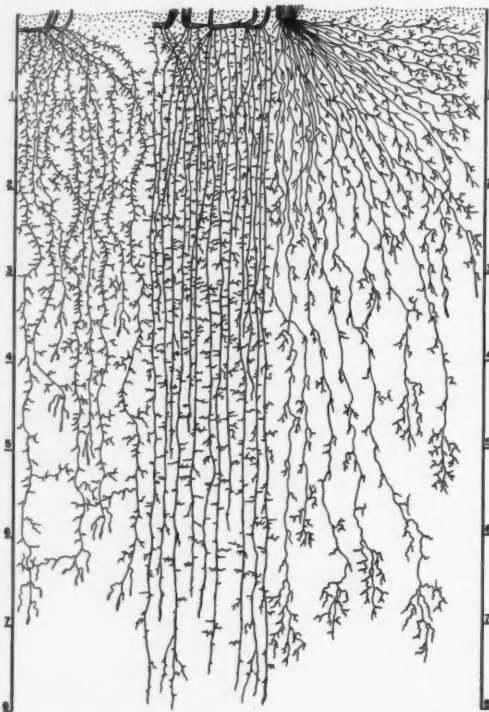


FIG. 8. Roots of dominant grasses growing in sand. From left to right they are sand bluestem (*Andropogon hallii*), sand reed (*Calamovilfa longifolia*), and little bluestem (*Andropogon scoparius*). Average number of roots in an in. layer of soil in a trench wall is shown from the shallowest to the greatest depth. Scale in feet.

Depths varying from 6-10 ft have been recorded in the many places where it and the following species were examined. The root branches, short and rebranched to the third or fourth order, are indeed numerous, sometimes 80/in. of main root.

SAND REED

Stems of sand reed usually arise singly from the strong root stocks and thus produce very open vege-

tation. The large panicles are held aloft 3-4.5 ft when flowering occurs in July to September. Long, mostly vertically descending roots arise from the coarse rhizomes on plants in stabilized vegetation, but others may spread widely (Fig. 8). Where the plants have been subjected to shifting sand, roots and rhizomes may be intermixed in dense mats to a depth of 2-3 ft. Root depth varies greatly, from 4.5-10 ft. Main roots are clothed throughout with multitudes of short, well-branched roots, that extend outward 1-3 in., mostly in a horizontal direction. Some roots, only 2-3 mm in diameter, end in starch-laden tips which are sometimes 8 mm thick. These occur on several other grasses growing in sand.

BLOWOUT GRASS

Redfieldia flexuosa is at home in shifting sand. It is found rarely in stabilized vegetation. The usually sparse and small clumps of a few stems each are connected by coarse, tough rhizomes which are 10-40 ft in length. The depth at which they occur depends upon the degree of burial by shifting sand—sometimes to 3-4 ft. Often they are exposed to great lengths on the sand surface. Whether horizontally, obliquely, or vertically placed, they produce numerous long roots densely clothed with short branches, which extend horizontally outward to vertically downward, some to depths of 5 ft or more. Thus, this pioneer adjusts itself to life in the shifting but moist soils of the sand dunes, where it forms very open but often nearly pure stands. The flexuose culms are 2-3 ft tall.

SANDHILLS MUHLY

Muhlenbergia pungens is a mid grass with strong but short rhizomes. It forms bunches 5-15 in. wide and may aggregate into large clumps. The tough, wire-like roots occur in clusters; some penetrate almost vertically downward to depths of 3-3.5 ft, others run off nearly horizontally a foot or two on all sides of the bunch, while the remainder pursue obliquely downward courses. Thus, a large volume of sand is occupied by roots. This grass forms open communities which replace blowout grass but in turn it is replaced by the more deeply rooted sand reed, sand bluestem and little bluestem in fully stabilized places.

LITTLE BLUESTEM

Root habit of little bluestem differs from that in true prairie in three ways. The main roots are less abundant, they spread more widely, especially in the surface soil, and penetrate more deeply in the sand (Figs. 4 & 8). In clay or silt loam the lateral spread of roots of little bluestem is normally only about 1 ft, but as the substratum becomes sandier the lateral spread and proportion of roots in the shallower soil increases. A maximum lateral spread of 3 ft may be attained. Its extreme range in depth from 3-4 ft in rock-filled soil to 8 ft in sand hills is indeed remarkable. The great plasticity of the root system is undoubtedly a factor accounting for its wide distribution.

OTHER GRASSES

Needle-and-thread (*Stipa comata*) has a root habit in sand not greatly unlike that described in hard lands. It has a wider lateral spread in the deeper sand and the main roots frequently break up into 3-5 profusely branched laterals. Depths of 4-5 ft are attained in stabilized vegetation.

Blue grama often roots 4.5 ft deep in sand; hairy grama (*B. hirsuta*) is much more shallowly rooted.

Sand lovegrass (*Eragrostis trichodes*) grows in widely spaced bunches on north slopes of dunes where it is protected from drying southerly winds. According to Tolstead (1942) the roots spread about 2 ft on all sides of the bunch in the surface foot but total depth did not exceed 2 ft. Junegrass and sun sedge (*Carex heliophila*) are also shallowly rooted.

From these typical examples of rhizome habit and root development, it may be concluded that, except for relatively few species, the usual root depth, lateral spread and nature of branching is well illustrated by the species shown in Fig. 8.

OTHER STUDIES IN SAND HILLS

A study of the root systems of various sand-hill communities and the environment under which the vegetation has developed has been made by Tolstead (1942), with findings in close agreement with those of the writer. He states that "the highly diversified and well developed vegetation of the dunes points to a great age and an early historical development of the sandhill flora." The tall sand-hill grasses are entirely characteristic of sand-hill habitats. Root habits in the several communities resulting from succession and degeneration are described.

DISCUSSION AND INTERPRETATION

Almost all the rainfall immediately enters the sand. After the storm, evaporation dries out the surface sand with great rapidity but to a slight depth only. An excellent mulch is formed by the layer of dry sand, which greatly retards further evaporation. Except in extreme drought, the sand at a depth of a few inches is nearly always moist. The efficiency of sand in absorbing rainfall without loss by runoff and in almost entirely preventing evaporation is the compensating factor which permits the growth of tall grasses.

Although growth of the dominant grasses occurs throughout the summer, and in dry years somewhat according to the occurrence of rain, flowering occurs in mid and late summer or autumn. Water loss from the sparse cover is undoubtedly much less than from upland true prairie. During summer there is probably little loss of water due to its penetration beyond the depth of the roots of the tall, postlimax grasses.

Tolstead found that pioneer vegetation in blowouts and communities in early phases of development were slow to deplete moisture. It was available throughout the growing season at depths beyond 2 ft. But xerophytic grasses in well developed communities with large leaf and root surfaces readily absorbed available moisture throughout the 4- to 5-ft levels and

endured long periods of drought. He concluded that the quantity of available moisture is the most important single environmental factor in determining the composition of the plant cover.

Ecological relations of the dominant grasses can be interpreted only after their underground relationships are understood. The tall grasses have stems widely spaced on their rhizomes and roots also are well spaced. In the several surface feet of sand they compete for water with more shallowly rooted species, such as hairy grama and sand dropseed, but they also absorb water at greater depths. During long periods of drought they may rely chiefly upon the deeper water supply. Although many sand-hills dominants thrive when grown in rich loam soil, they are unable to withstand competition of tall and mid grasses of true prairie growing in the sand-hill meadows. Moreover, most of them are too mesic to endure the severe competition of climax grasses of the hard lands.

The tall grasses, sand bluestem, sand reed and blow-out grass, all have rhizomes. Sand-hill muhly, a mid grass, also has strong rootstocks. Little bluestem and needle-and-thread are bunch grasses, but like the preceding species their roots extend deeply into the sand. Other important bunch grasses are sand lovegrass and sand dropseed. They are less deeply rooted. The short grasses, blue grama, hairy grama, and sun sedge, occur in the understory. Buffalo grass does not thrive in sand and occurs only rarely. The tufts and bunches of all the preceding grasses are so widely spaced in the several communities that basal area of vegetation is usually less than 5% except in compacted soil. Forage yield is much less than that of upland true prairie where 4 to 7 A support one animal unit. In the sand hills 17 A per animal unit are required.

ROOT-SOIL RELATIONS IN VARIOUS SOIL TYPES

Knowledge of the soil as a medium for growth of roots has increased very greatly in the past 30 yrs. Absorption of both water and nutrients at great depths has been adequately demonstrated (Crist & Weaver 1924, Hunter & Kelly 1946). Moreover, it has been found that during the period of heading and ripening of seed the deeper portions of the root system often absorb most actively. The monolith method, now widely used, permits the studying of the intimate relations of roots and soils and of measuring root production quantitatively at various soil levels. With a better understanding of the relationships of one soil type to another, and especially the greater accuracy and detail with which soil profiles are now described, it is possible to understand more fully the relationships between roots of grasses and the soil in which they grow.

The solum (A & B horizons) is especially important in root development, since most of the changes resulting from the growth of grasses throughout the centuries have occurred here. But roots of many grasses and especially perennial legumes, composites and

others, extend far into the C horizon as well. A deeply penetrating root system encounters numerous environments. Each may affect the nutrient, water, and air supply as well as the ease or difficulty of root penetration. The effects of these environments on a single representative root system, as revealed by the monolith method, afford an excellent opportunity for a study of problems relating to root distribution.

Approximately 50 monoliths with roots of 12 species of grasses from 16 different soil types have been studied and described in three general areas. One was in the vicinity of Lincoln near the Prairie soil—Chernozem boundary in eastern Nebraska. Another was 65 to 125 miles southwestward in Chernozem soils; the third was in the loess hills in central Nebraska where both Chernozem and Dark-Brown soils are found. Thus, root systems were obtained from many soils of widely different profile characteristics. Marked differences in root habit of the same species of grass growing in different soils were observed. Soil profile descriptions and photographs of roots taken from them are filed with the Soil Conservation Service of the U. S. Department of Agriculture, Lincoln, Nebraska (Weaver & Darland 1949, Weaver & Voigt 1950).

EXAMPLES OF ROOT HABITS IN AZONAL SOILS

A usual root depth of western wheatgrass in Zonal Prairie soil or Chernozem is 7-8 ft. Near Bruning, Nebraska, in Scott silty clay loam with a very compact claypan at 5-41 in. in depth, the root system occurred entirely in the first 31 in. of soil. In a well-drained Rendzina soil, near Belleville, Kansas, where the clayey subsoil overlaid unweathered limestone, roots extended downward only 38 in. In the loess hills near Kearney, Nebraska, roots penetrated the Colby silt loam, a Zonal Chernozem soil, to 10 ft. But on a hillside where the topsoil had been washed away and the fertility level was low in the thin, poorly developed new A1 horizon, the few roots produced by the dwarfed plants were only about 4 ft deep. Roots of blue grama responded in a similar manner in this azonal soil.

Buffalo grass in Holdrege silt loam of upland and in Wabash silt loam of lowland extended its roots downward to 6 and 6.5 ft, respectively, and produced more root-weight on the lowland. Root weight decreased with depth as is usual for all grasses in zonal soils. But in Sherman silt loam on a nearby hillside where there was a buried A horizon at 17 in. depth, there was an increase in weight in the second foot of soil over that in the second 6 in. This was probably due to the buried A horizon of an old soil.

Purple three-awn in zonal soil spread but little in the surface soil but distributed its roots below the plant to depths of about 4 ft. But in azonal loess soil only a few roots extended downward and 95% by weight ran outward horizontally in the surface 6 in. of soil, some to a distance of 3.5 ft. Since the soil was easily penetrable and moist several ft in depth, the response was undoubtedly due to a nutrient deficiency (cf. Voigt 1951).

Differences in soil compaction, water content, and amount of clay and nutrients, often cause marked differences in root development. The marked effects of soil upon root habits is especially pronounced where vegetation develops on intrazonal soils. These are soils with one or more horizons overdeveloped and in marked contrast to "normal" or zonal soils. Soils with claypans furnish excellent examples. In the Crete silty clay loam soil on a hillside near Lincoln, roots of western wheatgrass had three very different habitats. The A horizon, 14 in. thick, consisted of a black, mellow, well granulated silty clay loam. Here root development was similar to that in a zonal soil; about 500 main roots and their network of branches occurred in a foot-wide monolith 3 in. thick (Fig. 9).

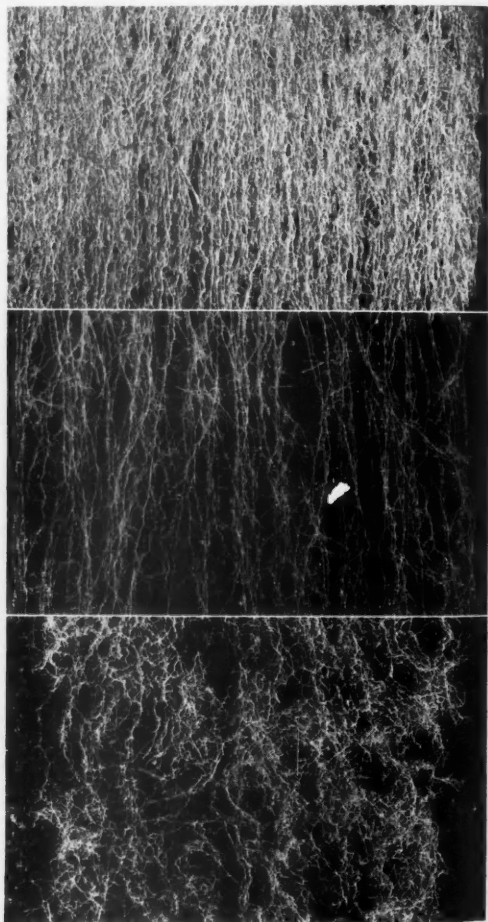


FIG. 9. Roots of western wheatgrass (*Agropyron smithii*) from a Crete silty clay loam soil with a claypan. They were in a foot-wide monolith 3 in. thick from the central portion of the A horizon (upper), the central part of the B horizon (middle), and the lower portion of the C horizon (lower). Roots are about one-fourth natural size.

A very distinct and abrupt transition to a blocky prismatic structure occurred in the B horizon, which was 16 in. thick. Clay content increased rapidly with depth. The vertical prisms were 8-12 in. long and 3-4 in. thick. The soil was very heavy and although moist it was removed only with great difficulty. Only about a third of the roots entered this claypan and the number that continued into the C horizon was only about half as great. Some roots penetrated downward through the prisms, despite their compact structure, but many grew downward on their surfaces and were attached to the soil only by their finer branches. Here they branched abundantly but only in one plane.

The C horizon consisted of loess, a silty clay loam of massive structure. It was mellow and moist and contained an abundance of lime, often in concretions. The soil broke up into blocky pieces. This offered a third environment for root development, and the type of root distribution was distinctly different from that in either the A or B horizon. The roots were often flattened on the faces of small blocks which cleaved in all directions; a few penetrated into the blocks. Thus, these white roots branched in all planes and, when freed from soil, appeared as a glistening white mass (Fig. 9). Often greater root development occurs below the claypan than within it. The root weight in this sample in the first foot of the C horizon was 30% greater than that in the lower foot of the B horizon.

SEGREGATING FACTORS INFLUENCING DISTRIBUTION

Although it is difficult to segregate the various physical and chemical factors that influence root penetration and distribution, yet it seems certain that the surface environment is only one set of conditions which influence root development. A study has been made of some physical and chemical properties of several prairie soils and related to the distribution of grass roots. Marked variations in profile characteristics, and abrupt boundaries between horizons, especially with regards to physical properties were found in Crete and Butler soils. "In a Butler soil near Carleton, Nebraska, limited root development of western wheatgrass in the upper region of clay accumulation was a feature of this profile. A reduction of branching was observed at a depth of 8 in. and extended to a depth of 20 in. Associated with this was a greatly reduced phosphorus supply and a restricted pore space. Increased branching of roots in the lower B horizon (20-28 in.) was associated with an increased percentage of pore space and with a soluble phosphorus content of nearly 2.5 times that present in the region of restricted development. Root weight was one-third greater in the lower B horizon within the depth of 20-28 in., than the weight of roots from an equal volume of soil in the region of restricted growth" (Fox, Weaver & Lipps 1953).

Effects of different soil types on root distribution are often great. Roots of Kentucky bluegrass and blue grama were studied in a compact Carrington silty clay loam, and in a deep, well drained Judson

silt loam, a type occurring between upland soils and alluvial bottom lands. The Carrington was an old soil developed on glacial soil before the Peorian loess was deposited upon it. The A horizon was 7 in. deep and the B horizon extended to only 22 in. The entire solum, though granular in structure, consisted of heavy silty clay loam. It was very compact and water penetration was poor. In the Judson soil the A horizon of the mellow granular silt loam was 20 in. deep and the granular silty clay loam of the B horizon 10 in. deeper. Silty clay then occurred to the depth of the solum at 4.5 ft. These two stations were only a few miles distant from Lincoln.

The differences in root penetration, 22 in. in Carrington and 48 in. in the Judson soil reflect wide differences in soil properties. Moreover, the bulk of the roots, about 82% by weight, were confined to the upper 7 in. in the first type. The deep A horizon (0-20 in.) of the Judson soil was filled with a great mass of roots with a total weight more than 3.5 times as great as that in the shallower soil.

"Total pore space in the 0-4 in. depth of the Carrington soil was somewhat less than at a similar depth in the Judson soil; but throughout the remaining depths, percentage of pore space and clay content in the two soils were not greatly different. The total nitrogen content of the Carrington was lower than in the Judson soil. Soluble phosphorus content was extremely low in the Carrington soil; and at a depth of 20-24 in., which marks the deepest penetration of roots, the level of phosphorus was only 10% of that at the same depth in Judson soil.

"The Judson soil was well supplied with mineral nutrients at all depths. Although the soil was slightly acid, the exchangeable bases were sufficient for plant nutrition and nitrification of organic matter. Total soil nitrogen was high and the phosphorus level in the surface soil was sufficient throughout the profile to promote excellent root development at all depths.

"In the Carrington soil, only the levels of calcium and magnesium appeared to be optimum for root growth. The soluble phosphorus content was extremely low. The exchangeable potassium was also very low . . . and it may have been a limiting factor in root growth" (Fox, Weaver & Lipps 1953).

ROOT DEVELOPMENT AND REMOVAL OF TOPS

One of the most important factors affecting root development of grass does not occur in the soil. It is frequent removal of parts above ground as in overgrazing. During the dry year of 1933 it was noticed that native grasses in long-overgrazed prairie protected during recovery were much more subject to wilting than were plants in adjacent prairie that had not been grazed. The leaves rolled or folded and many of the lower ones dried and lost their green color. The evidence pointed clearly to a meager or inefficient root system. Accordingly experiments on effects of frequent removal of tops on development of the root system were performed.

Large blocks of sod of 10 species of the more

abundant prairie grasses were grown at Lincoln each in large, deep containers under favorable conditions. Grasses in one-half of the containers were clipped as if closely grazed about 7 times during the growing season. The clipped plants failed to produce new rhizomes and many of the old ones died. Roots developed very poorly in length compared with the unclipped controls. Both volume and dry weight of roots were greatly reduced, the average volume to 12% and the average dry weight to 10% of the controls. Moreover, the diameter of the roots was only about three-fourths, or less, than that of unclipped plants (Biswell & Weaver 1933).

When transplanted blocks of sod of various prairie grasses were placed under control conditions for study, it was ascertained that those which were clipped four times during the six weeks they were producing new tops developed few and sometimes no roots (Weaver & Darland 1947). In the Great Plains the grass roots were greatly affected by close clipping (Albertson, Riegel & Launchbaugh 1953). Many similar studies are discussed in the three papers just cited.

A prairie of 290 A near Lincoln had been grazed moderately but not uniformly for more than 50 yrs. The soil was Carrington silt loam, quite uniform throughout. After several years of study the 3 range-condition classes it presented—excellent, good and fair—were mapped. In the excellent class both big and little bluestem had not been harmed by too frequent and too close grazing. In the mid-grade (good) condition both grasses showed some overuse by more open bunches, less remaining stubble, and less debris from preceding forage crops. Some bluestems still persisted in the low-grade (fair) condition class which was nearer the water and salt supply and, consequently, most often grazed. They were in a much weakened condition.

A representative bunch of little bluestem and a sod of big bluestem were selected in each range condition class. Monoliths of the soil under each were procured and examined. The results showed a decrease in root weight of 55% in mid-grade and 75% in fair grade pasture. Root deterioration was from root tips upward toward the crown. Deterioration in big bluestem was about the same as that of little bluestem. Decrease in dry weight was 49% in mid-grade pasture and 76% in fair grade (Weaver 1950).

In poor pasture all bluestems had disappeared. They were replaced by Kentucky bluegrass and blue grama neither of which utilized the moisture and nutrient supplies to a depth greater than 2.5-3 ft.

Decrease in weight of total underground parts of grasses when little bluestem prairie had been reduced by overstocking to an early, a medial, and a late stage of degeneration has been ascertained. Samples from pastures in early, medial, and late stages of degeneration showed consistent decreases in underground plant materials. On upland, decreases in dry weight were 35, 40 and 72%, respectively, from the original

sod in the surface 0-4 in. Similar decreases occurred at the 4-12 in. depth.

It has recently been shown that removal during the growing season of half or more of the foliage of various grasses—including switchgrass and blue grama—caused root growth to stop for a time after each removal (Crider 1955). "A single clipping that removed most of the foliage caused root growth to stop for periods ranging from 6 to 18 days. Stoppage occurred usually within 24 hrs and continued until recovery of the top growth was well advanced. . . . The percentage of roots that stopped growth varied in proportion to the percentage of the foliage that was removed. . . . Stoppage of root growth failed to take place . . . only when 40% or less of the foliage was removed."

Root-soil relations in various soil types and root development and removal of tops both illustrate the need of some understanding of differences between successional stages and stabilized or climax vegetation and especially that of zonal and azonal soils. It was only with the cooperation of the Soil Survey of the Soil Conservation Service at Lincoln, Nebraska, and the Department of Soils of the University of Nebraska that this part of the study was possible. The diagrams of underground parts in the several communities illustrated are believed to represent the usual plant development in each throughout the very extensive territory described. From the studies of others, notably Hanson & Whitman (1938), it may be that the patterns extend over even much wider grassland areas.

SUMMARY

Underground development in western Iowa, Nebraska, Kansas and eastern Colorado has been studied for a period of 40 yrs. The earlier work (1916-1927) dealt largely with the root systems of a large number of individual species in relation to soil and climate. In further intensive studies of the structure of prairie vegetation this background was employed in defining the root habits of various plant communities on fully developed and stabilized soils. Both soil and aerial environment determining root development were used in interpreting community root habits.

Studies of the effects of extreme drought, recovery from drought, and removal of herbage on root development have aided greatly in the interpretation. They also emphasized the value of a knowledge of the usual community root habit.

The sod-forming tall grasses of lowland communities of true prairie are of the greatest height (5-10 ft), have the greatest leaf surface, and produce the largest amount of forage. Their roots are coarsest, least well branched, but deepest. They are about as deep (7-10 ft) as the stems are tall. Roots do not spread widely just below the soil surface. All of the dominants, except *Elymus canadensis*, are warm-season grasses that grow all summer and flower late.

Upland mid grasses nearly all grow in bunches. They are of intermediate height (2-3.5 ft), leaf surface, and amount of forage production. Roots are

moderately fine, well branched, and moderately deep. They are about twice as deep (4-5.5 ft) as the stems are tall. They are fairly well spread and moderately dense just beneath the soil surface. Grasses from lowland when growing in upland are reduced in size and weight. The roots are somewhat finer and more branched but penetrate less deeply. There are several cool-season grasses on uplands which flower early but most are warm-season species, flowering late after a long season for growth.

Grasses of the hard lands of mixed prairie are the smallest in height, leaf surface, and amount of forage production. Mid grasses are usually 1.5-2.5 ft high and short grasses of the understory 4-15 in. Both groups are represented by bunch grasses and sod formers. Roots are finest, best branched, and about as deep as those of upland true prairie. But they are 2-16 times deeper than the stems are tall. They spread widely and form dense masses in the surface soil and nearly all are well branched throughout. When hard-land species grow in true prairie they increase in size and weight. The roots are often deeper, spread much less in the surface soil and branch less profusely. All of these grasses are extremely xeric. Many cool-season grasses and sedges may evade drought by early growth and flowering. Warm-season grasses may grow intermittently, when water is available. All can undergo deep drought-dormancy and revive when rains come.

The amount of roots, stem bases and rhizomes in the surface 4 in. of soil is greatest in lowland of true prairie (3.7 T/A), intermediate in upland true prairie (2.7 T/A), and least in the hard lands in mixed prairie (1.8 T/A). This cover of sod has protected the surface of the earth for centuries against violent physiographic change and has made possible the formation of soil.

Grasses of mixed prairie in the Loess Hills, under a precipitation of 23 in., are usually rooted 2-4 ft deeper than those in adjacent hard lands. This is due to deeper water penetration and perhaps also to a higher percentage of readily soluble phosphorus.

Postclimax tall grasses in sand grow higher (4-5 ft) than grasses of upland true prairie. The mid grasses equal or exceed in height those of mixed prairie hard lands. They are mostly warm-season grasses, but some cool-season species are common. Sand-hills grasses are characterized by moderately fine roots which spread widely in the surface, usually 1.5-3 ft, and penetrate deeply, mostly 4-7 ft. The roots have extremely numerous branches, often 15-75 per in., mostly only 0.5-3 in. in length, but longer ones may occur in the deeper soil. Branching of these fine rootlets often occurs to the third or fourth order. Grasses that grow both in sand and silt loam spread their roots more widely in sand but usually not so close to the soil surface. Several grasses found only in sand have excellent rhizomes. The cover of vegetation is more open and forage production is much less than that of upland true prairie but may equal or exceed that of plains hard lands.

Over much of the prairie and plains, because of good soil structure, slight leaching, and almost negligible fertilizer requirements, the quantity of water demanded by the richness of the soil usually exceeds the supply and thus water becomes the limiting factor to plant growth.

Grassland vegetation is adjusted to fit into periods of dry cycles as well as wetter ones. Reserves of food in crowns, rhizomes and roots are extensive and the ability to absorb water throughout a large volume of soil is excellent.

Soil-root relationships in various soil types are considered. A study of intrazonal and azonal soils by the monolith method has made clear some of the physical and chemical causes for root variations.

The extremely important relation of root development to removal of tops has been discussed, especially as it is affected by various degrees of grazing.

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THE ROLE OF REPRODUCTION AND MORTALITY IN POPULATION FLUCTUATIONS OF VOLES (*MICROTUS*)

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INTRODUCTION

Fluctuations in the density of animal populations are well-nigh universal, yet the nature of these fluctuations is quite diverse, and some are poorly understood. Change in population density is due to the interaction of additive forces—immigration and birth, on the one hand, and of subtractive forces—emigration and death, on the other. Where movement is of slight importance in influencing population density, births and deaths in the population then play the major role in determining the pattern of increase or decrease. It has thus become a truism that an animal population increases in numbers when the birth rate exceeds the death rate, and decreases in numbers when the birth rate falls below the death rate. The fluctuations may be seasonal (annual) due to discontinuous recruitment of new individuals and to seasonal variations in mortality. But fluctuations in numbers from year to year (multi-annual) are also found, and these have proven more difficult to explain than seasonal changes in density.

Certain multi-annual fluctuations have attracted attention because of the seeming regularity with which the population reaches a peak density and then declines, only to build up to another peak. The regularity, plus the large amplitude of population change, has earned for this type of fluctuation the name "cycle." Although some authors have criticized the rather loose usage of the term, it carries the weight of tradition, and will be used in the following discussion as applying to the year-to-year fluctuations in density of vole populations.

Among the diverse observations that have been

made on the biology of the "microtine cycle," one of special interest and potential significance is the relationship between reproduction, or more specifically, the natality rate of the population, and the fluctuating density of the population. Hamilton (1937a) and Bodenheimer (1949) report that natality increases during the period of population build-up and decreases during the period of population decline in *Microtus pennsylvanicus* and *M. gambelii*. Increased litter size, increased breeding rate, and a longer breeding season were the components of reproduction thought to contribute to increased natality during the "increase" phase of the cycle, and these same components suffered reduction during the "decrease" phase. Thus, natality was directly related to vole population density in these two studies, and the authors believed the fluctuating natality rates to have played a major role in causing the observed density fluctuations. This viewpoint does not take into sufficient account the possible importance of a relationship between population density and mortality rates. It is the interplay of natality and mortality, particularly during the breeding season, which must be the immediate cause of population growth or decline.

The present study was designed to investigate this reported relationship between natality and population density, and to assess the relative importance of reproduction and mortality in population fluctuations of voles. This report is part of a recently completed study of population fluctuations in the so-called "primarily cyclic species"—the microtine rodents and the northern grouse and hares. It includes only the details of reproduction and mortality in two species of California voles. Other aspects of the population

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fluctuations in the voles, and in sooty grouse and snowshoe hares will be presented elsewhere.

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METHODS

The montane vole, *Microtus montanus*, and the California vole, *M. californicus*, are approximately the same size, and occupy similar ecological niches; they are the most common small grazing rodents in their respective ranges. Even though there is some overlap in range in northern California, the two species are separated altitudinally. *M. californicus* is found in lowland grasslands, while *M. montanus* occurs in mountain meadows. The *M. montanus* population that I studied inhabits a region of climatic extremes—long, cold winters with continual snow-cover, and short, hot summers with occasional thunder showers. Winter is the non-breeding season. In contrast, the *M. californicus* population investigated is not subject to temperature extremes, and the major seasonal cycle is one of rainfall. Lack of rain in the late summer and early fall curtails breeding during this period.

Microtus montanus was studied in the vicinity of the University of California's Sagehen Creek Experimental Station, located in Nevada County, California, on the east slope of the Sierra Nevada. The station is 10 mi north of the town of Truckee, California, at an elevation of about 6600 ft. Vole populations were studied in six mountain meadows of various size, bordering Sagehen Creek. Each meadow was isolated from the others by tracts of montane forest and by the creek, and these barriers are believed to prevent movement of voles from one meadow to another on a scale which would affect population densities. All meadows were undisturbed except for the passage of a band of 1600 sheep through them each

summer, to and from their pasturage at higher elevations. In addition, two of the meadows were treated with commercial fertilizers in the summer of 1954. An analysis of this treatment will be published later. *Microtus californicus* was studied in Tilden Regional Park, Contra Costa County, California. The park lies just east of the city of Berkeley, and the elevation of the study area ranges from about 600 to 1200 ft. Voles here were studied in two separate areas more than a mile apart, one being annual grassland, and the other mixed grass and chaparral. Both areas were free of disturbance, although a grass fire in October, 1953, burned to within a few hundred yards of one area.

All vole populations were sampled periodically by means of Museum Special snap-traps along standardized NACSM lines as proposed by Calhoun (1948). NACSM trap lines consist of 20 trap stations, each with three traps placed around it, set for a three-day period. Two pairs of type B lines were used in Tilden Park. They had an interval of 50 ft between trap stations, and traps at each station were set within a 5-ft radius. These lines were established in 1950 by D. H. Brant. At Sagehen Creek, three parallel type A lines, with a 25-ft interval between stations and a trapping radius of 2.5 ft around each station, were established in 1952. In 1953, another pair of type A lines and a pair of type B lines were added. In addition, unsystematic trapping was carried on at different times to obtain samples for seasons other than the NACSM trapping periods. The population of *M. montanus* was trapped from June, 1952, through June, 1955, while that of *M. californicus* was trapped from March, 1953, through August, 1955. Complete data on all mice trapped will be published in NACSM Releases, and may be consulted there.

Autopsy of trapped voles yielded a variety of data. Fresh, or "active" corpora lutea could easily be counted in the ovaries of pregnant or lactating female voles. Each ovary was dissected with needle and fine forceps until the corpora lutea were all separated from one another, to facilitate counting, and counts were made with a binocular dissecting microscope. These corpora lutea counts may not be perfectly reliable. Allen, Brambell, & Mills (1947: 322) found an experimental error of 6.8% in counts of corpora lutea in ovaries of wild rabbits, due mainly to omissions. Corpora lutea in voles are so much larger relative to the ovary than in the rabbit, however, that the error in counts is probably less than this. If each fresh corpus luteum is assumed to have arisen from a recently ovulated follicle, then corpora lutea counts are a measure of ovulation rate. This was suitable for *M. montanus*, in which accessory corpora lutea did not appear to form, but not for *M. californicus*, in which a variable number of accessory corpora, of uncertain origin, appeared in the ovaries.

The number and size of normal and resorbing embryos was also determined for each pregnant

female. All females were examined for presence and number of placental scars. A placental scar forms at the implantation site of the embryo and is marked by the presence of a metrial gland or an area of black pigmentation on the mesometrial side of the uterus. Since each placental scar corresponds to an implanted embryo, placental scar counts also give an approximation of litter size. Scar counts in primiparous females are considered reliable, since Conaway (1955:530), working with laboratory rats, found that "the number and distribution of placental scars was always equal to the number of viable embryos present on approximately the eighth day or eleventh day of pregnancy depending on the type of resorption that occurred." Furthermore, Davis & Emlen (1948:166) found that scars did not occur in virgin laboratory rats and were persistent in all parous rats. However, interpretation of scar counts in multiparous females is probably less reliable. A comparison of the number of placental scars with the number of young produced in the laboratory rat (Davis & Emlen *op. cit.*: 163) produced a discrepancy between the two counts of several hundred percent in either direction. Fewer young than scars can be attributed to prenatal mortality, while fewer scars than young are considered due to superposition or fusion of the scars of successive litters.

In a wild vole population it is probable that only an occasional multiparous female produces more than 2-3 litters. Thus there is a lower probability that implantation sites will be superposed in these voles than in laboratory rats that have been "repeatedly bred" (Davis & Emlen *op. cit.*: 162). When scar counts were made on voles in the present study, scars were classified into two categories. "New" scars are those in actively breeding females (pregnant or lactating) corresponding to the most recent litter produced. This would include scars in breeding primiparous females, and the latest set of scars in multiparous females. "Old" scars are those in non-breeding females, and older sets in breeding multiparous females.

Other data, such as amount of mammary tissue, size and prominence of nipples, presence of expressible milk, general condition of ovaries and uterus, and closure of vagina and pubic symphysis, were also recorded for each female examined.

Testes size, and size and condition of seminal vesicles and epididymis were noted for each male vole captured.

Finally, weight, total length, tail length and pelage condition were recorded for all specimens, for use as age criteria. One chronic difficulty in population studies of mammals is the lack of adequate criteria of age, and this is particularly true in studies of microtine rodents. Pattern of tooth wear is not usually used because the teeth in most genera continue to grow from a persistent pulp, although Zimmermann (1937) employed it for *Clethrionomys* in which adults develop rooted molars. Bodenheimer (1949:54) used the weight of the lower jawbone to age *Microtus guen-*

theri, and Sperber (1948:2) measured the length of the upper molar row in *M. agrestis*. However, the majority of workers have used total body weight as an index of age (Naumov 1936:158; Jameson 1947:44; Chitty 1952:514; Greenwald 1957:422; Bee & Hall 1956:94, 99). Howell (1924:982) concluded that weight showed the best correlation with age as determined by skull measurements in *M. montanus*. Laboratory studies of *Microtus* spp. by Cowan & Arsenault (1954:201), Hamilton (1937b:503; 1941:12), Hatfield (1935:238), and Selle (1928:97), and field studies by Barbehenn (1955:534ff.) and Martin (1956:388ff.) indicate that variations in weight-gain are relatively slight, at least for the first month of life. Thereafter variability increases, but not, I believe, to the extent that weight measurement becomes useless, particularly since population-wide seasonal variability may be corrected for.

The criteria of age used in the present study are weight, body length, and type of pelage. The weight and body length of every individual were plotted for each sample. In each sample, there were generally clear breaks between three groups, especially in *M. montanus*, which were designated as adult, sub-adult, and juvenile. In both voles, sub-adults weighed more than 20-25 g, and adults weighed more than 35-40 g. Juveniles have a pelage that is uniformly grey ventrally and brown dorsally. Sub-adult pelage is a light silver-grey ventrally, and dark grey above. Adults have a more markedly agouti grey above and below; the dorsal and ventral coloration tends to blend, whereas sub-adults are bicolored in appearance. The classification into three age groups on these bases is considered reasonably accurate.

POPULATION FLUCTUATIONS

Fig. 1 summarizes the variation in numbers observed in populations of the two species during the study. While the number of voles captured by a standard trap line cannot safely be interpreted in terms of actual population density, the catch serves as a fairly reliable index of seasonal and year-to-year changes in gross abundance of the voles.

From a low density in 1951, the *Microtus montanus* population built up through 1952 to a peak in the fall of 1953, and then suffered a sharp decline, or "crash," in 1954. However, with the possible exception of 1955, the densities of the populations each spring, prior to the birth of young into the population, were approximately equal in each of the years of study. The level of population at this season has been termed "primary density" by Varshavskii, Krilova, & Luk'yanchenko (1948:959). The main difference from year to year in numbers caught was in the fall. This fact indicates that reproduction and survival during the breeding season determined whether the population reached a "cyclic" peak, increased moderately, or declined.

Populations of *M. californicus* also exhibited this tendency to return to a base population level prior to the onset of a new breeding season, i.e. there was little difference in "primary density" from year to year.

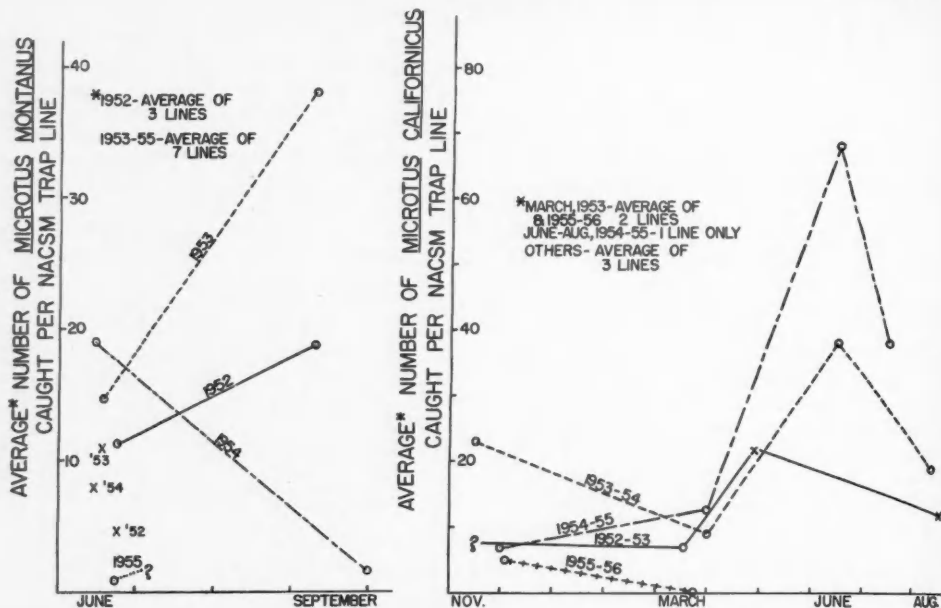


FIG. 1. Trend of numbers in vole populations as measured by catch on NACSM lines (60 traps per line; 3 day trapping period). O—adults and young; X—adults only. Left, *Microtus montanus* population in mountain meadows at Sagehen Creek, Nevada County, California. Right, *Microtus californicus* population in upland annual grassland at Tilden Regional Park, Contra Costa County, California.

But the density of population at the end of each breeding season showed a progressive increase from 1953 to 1955, being moderate in the summer of 1953, somewhat higher in 1954, and reaching a very high density in the summer of 1955. Following this "cyclic" peak, no voles were caught in the spring of 1956 (O. P. Pearson personal communication), suggesting that a population "crash" had occurred. Thus, the peak density of the *M. californicus* population occurred in 1955, at which time the *M. montanus* population, which peaked in 1953, was at a low ebb.

These trends of vole abundance constitute the basic frame of reference for discussing the role of reproduction and mortality in the microtine cycle.

REPRODUCTION

That microtine rodents, which have pronounced short cyclic fluctuations in numbers, also have the highest mammalian reproductive potential, is pertinent to understanding the nature of these fluctuations. Females of the genus *Microtus* are polyestrous and have a postpartum heat; *M. californicus* and *M. montanus* are of this type. These characteristics, plus a short gestation of 21 days (Hatfield 1935:264) and rapid attainment of maturity in both sexes, give the species a potentially high intrinsic rate of natural increase.

OVULATION RATE

The number of fresh corpora lutea in the ovaries of pregnant or lactating females was counted to de-

termine the rate of ovulation in the Sagehen Creek and Tilden Park populations.

M. montanus. The mean number of corpora lutea in 194 females was 6.75, with a range of 1-13. Seasonal and year-to-year variation is presented in Table 1. The difference between 1952 and 1953-54 is significant ($P < .01$). In 1952, the population was at medium density, and in 1953 at a high density. In most of the samples ovulation rate is inversely related to the density, this inversely being especially marked in September, 1953. An exception is ovulation rate in 1954 which does not differ from that in 1953, even though the population was rapidly declining after late spring. The failure of ovulation rate to increase as population density decreased, as would be expected of an inverse relationship, might be related to the ensuing "crash" of the vole population. However, the year-to-year differences in ovulation rate do not seem of sufficient magnitude of themselves to account for the marked changes in numbers of the voles.

There is a consistent seasonal trend in corpora lutea numbers, the ovulation rate being highest at the beginning of the breeding season, and progressively declining to the end.

M. californicus. The number of corpora lutea in the ovaries of *Microtus californicus* is not a reliable criterion of ovulation rate because of the formation of accessory corpora in many individuals. Greenwald (1956:218) states that the numbers of these accessory corpora bear no relation to previous reproduction or to embryo size, and that the largest numbers are

TABLE 1. Seasonal and year-to-year variation in corpora lutea counts and litter size in mature¹ females of *Microtus montanus* and *M. californicus*.

Mean Sampling date	MEAN NUMBERS								
	Corpora lutea			Embryos			Placental Scars		
	N	M	S. E.	N	M	S. E.	N	M	S. E.
<i>A. Microtus montanus.</i>									
1952 June 24.....	9	8.89	± .20	5	7.80	± .49	4	7.75	± .48
July.....				no sample					
Sept. 10.....	19	6.63	± .27	11	5.45	± .43	8	5.75	± .31
1953 June 11, 24 ² .	48	7.70	± .20	44	7.16	± .22	5	7.00	± .45
July 31.....	12	6.17	± .32	7	6.57	± .37	13	6.30	± .46
Sept. 6, 10.....	34 ³	4.76	± .22	11	4.09	± .28	27	5.93	± .26 old
							24	5.21	± .17 new
1954 June 12, 18.....	43 ⁴	7.81	± .20	19	7.42	± .34	16	7.00	± .44
July 11.....	12	6.08	± .44	9	5.22	± .40	5	6.00	± .71
Sept. 30 ⁵	8	4.63	± .42	2	3.00	6	4.00	± .38
1955 June 23.....	1	10.00	1	9.00	0
<i>B. Microtus californicus.</i>									
1953 Mar. 16.....	8	10.50	± .57	8	6.00	± .63	1	7.00
Apr. 21.....	10	16.70	± 1.70	11	6.40	± .76	1	7.00
Aug. 17.....	1	4.00	0	2	3.50
Nov. 10, 15.....	40	6.00	± .63	8	3.13	± .29	18	3.61	± .26 old
							16	3.36	± .20 new
1954 Mar. 21.....	12	9.08	± 1.34	8	5.38	± .50	5	4.80	± .73
Apr. 14.....	2	18.00	2	6.00	0
Nov. 25.....	11	6.00	± 1.31	6	3.00	± .26	2	3.50
							3	4.00	old new
1955 Feb. 14.....	6	10.83	± 2.41	5	4.40	± .26	2	4.50
Mar. 19.....	10	18.10	± 2.65	6	5.33	± .71	7	5.00	± .43
Apr. 7.....	12	13.42	± 3.79	7	5.71	± .29	4	4.75	± .25
June 15.....	20	7.80	± 1.38	11	3.91	± .55	13	5.00	± .23
July 14.....	4	5.00	± 1.42	0	5	3.40	± .40
Aug. 10.....	0	0	4	2.75	± .13

¹Figures refer to only that portion of females in the sample that contain either corpora lutea, embryos, or placental scars. Immature females are not included in calculation of mean values.

²Includes 4 pregnant females trapped June 7.

³Includes 11 females with corpora, but no embryos or scars.

⁴Corpora regressed in 13 females; not countable.

⁵Sample from fertilized meadow.

restricted to the main breeding season. Findings in the present study in general do not contradict this. The seasonal and year-to-year variations in numbers of corpora lutea are given in Table 1. The number of corpora is low in November, at the beginning of breeding following the late summer pause. This indicates very little formation of accessory corpora. Mean number of corpora increases as the breeding season continues in all three years, and the variance in the samples also increases. There is no difference between the counts in 1953 and 1954, but in March, 1955, the number of corpora was significantly higher than in samples of the previous years, and then declined as the intensity of breeding actively declined. Fifty-five primiparous females had a mean corpora lutea count of 12.15, while 43 multiparous females had a count of 12.35, not significantly different; both classes of females have the same seasonal pattern of change.

Since ovulation rates in *M. californicus* cannot be determined, no comparison with *M. montanus* can be made. However, as with the montane vole, there is no evidence that ovulation rate is causally related to the population cycle in *M. californicus*.

EMBRYO NUMBERS

The number of normal embryos visible in all pregnant females was counted to give an approximation of the litter size.

M. montanus. Mean embryo number was 6.47 for 109 females, with a range of 2-10. The seasonal and year-to-year variation is shown in Table 1. Significant changes in embryo counts occur in two sets of paired (seasonally comparable) samples, litter size being lower in September, 1953, than in September, 1952, and lower in July, 1954, than in July, 1953. This is, in part, contrary to what Hamilton (1937a: 785) found in *Microtus pennsylvanicus*, in which lit-

TABLE 2. Seasonal progression of litter size in *Microtus montanus* and *M. californicus*.

	A. <i>Microtus montanus</i> .				Evidence used
	1952	1953	1954		
June.....	7.75 ± .48 7.80 ± .49	7.00 ± .45 7.16 ± .22	7.00 ± .44 7.42 ± .34		New scars Embryos
July-Aug.....	no sample no sample	6.30 ± .46 6.57 ± .37	6.00 ± .80 5.22 ± .40		All scars Embryos
Sept.....	no sample 5.75 ± .31 5.45 ± .43	5.93 ± .26 5.21 ± .17 4.09 ± .28	no sample 4.00 ± .38 3.00		Old scars New scars Embryos
	B. <i>Microtus californicus</i> .				Evidence used
	1952-53	1953-54	1954-55		
Nov.....	no sample	3.36 ± .20 3.13 ± .29	4.00 3.00 ± .26		New scars Embryos
Feb.....	no sample	no sample	4.50 4.40 ± .40		New scars Embryos
Mar.....	7.00 6.00 ± .63	4.80 ± .73 5.38 ± .50	5.00 ± .43 5.33 ± .71		All scars Embryos
April.....	7.00 6.40 ± .76	6.00	4.75 ± .25 5.71 ± .29		All scars Embryos
June.....	no sample	no sample	5.00 ± .23 3.91 ± .55		All scars Embryos
July.....	no sample	no sample	3.40 ± .40		All scars
August.....	3.50	no sample	2.75 ± .13		Old scars
Nov.....	3.61 ± .26	3.50	no sample		Old scars

ter size was higher in the peak year than in the preceding or following years. Bodenheimer (1949:46) also claims that "average litter size was 6 to 14" during the period of build-up in *Microtus guentheri*, as against 3 to 8 in normal years.

There is some indication that embryo numbers may actually have been higher in June, 1952, than in the subsequent springs, thus following the pattern found in ovulation rate, which also was higher in 1952. The small sample in 1952 makes the matter uncertain, but if it is true the higher value occurs in the year prior to the population peak, rather than in the peak year. The low average for embryo counts in September, 1953, is explainable simply as an inverse response to the peak population density of that period, but the low value in the July, 1954, sample may reflect some sort of cyclic depression acting on litter size during the period of the crash decline. Such a depression would corroborate Hamilton's observation that mean embryo numbers were higher in the peak year than in the year of decline, but the decrease in natality does not seem sufficient to be a major cause of population decline.

The pattern of seasonal variation in embryo num-

bers is identical to that of ovulation rate, with a progressive decrease as the breeding season continues.

M. californicus. The mean embryo number for 73 pregnant females was 4.94 with a range of 1-10. This is somewhat higher than the mean number of 4.20 found by Greenwald (1956:213) in a population inhabiting the edge of *Salicornia* salt marsh along San Francisco Bay.

Seasonal and year-to-year variations are shown in Table 1. There is no significant change in litter size during the population cycle, although the decline in the March and April samples from 1953 to 1955, when the voles were building up to a peak, might be significant if the samples were larger. Greenwald (1957:435, 442) reports an inverse relationship between population density and litter size in *M. californicus*.

PLACENTAL SCARS

M. montanus. Mean placental scar number, counting only new scars, for 75 females was 6.02. Table 1 gives the seasonal and year-to-year variation. As with embryo numbers, no significant difference occurs between the years in the June samples, although litters were probably larger in 1952. A significant

decrease again occurs between June and September in all years.

In comparing placental scar counts with embryo counts, it should be remembered that the scars correspond to litters that have preceded the litters *in utero* in the same sampling period. This allows one to arrange litters chronologically, using scars and embryos (Table 2).

If the data from scars and embryos for the June samples are combined, the mean litter sizes for 1952, 1953, and 1954 respectively become $7.78 \pm .32$, $7.15 \pm .20$, and $7.24 \pm .27$. The difference between the first two years approaches significance ($.08 < P < .10$), but this difference in mean litter size (.63) is only about half the difference between ovulation rates for the same two years (1.09). If the July samples in 1953 and 1954 are similarly combined, mean litter size for these two years becomes $6.40 \pm .32$ and $5.50 \pm .36$, respectively. Combining of the September data for these same years indicates a litter size of $5.58 \pm .28$ in 1952, $5.32 \pm .16$ in 1953, and $3.75 \pm .41$ in 1954. This further strengthens the view that litter size was, for some reason, depressed during the period of rapid population decline in 1954.

On the basis of data available, natality in *Microtus montanus* holds a generally inverse relationship to population density. Ovulation rate and litter size were greatest in 1952, when density was moderate and the cycle was in the increase stage. In 1953, and through the spring of 1954, vole populations were at the peak of the cycle, and natality was reduced. In the summer and fall of 1954, natality declined still further even though the population density was declining. Thus, in this "crash" period the inverse relationship between natality and population density failed to hold. Increase in natality rate, then, is not a direct cause of cyclic increase in this case, but the cyclic decline may have been aided by reduction of litter size, although this cannot be the whole reason for the population decrease.

M. californicus. The mean number of new placental scars found in 42 females was 4.29; of old scars in 35 females, 4.17. The seasonal and year-to-year variation is given in Table 1. By using both embryo and placental scar counts, one can see that litter size increases from about 3 at the beginning of the breeding season in November to a peak of about 6 in April, and then declines during the last part of the season to 3 or 4 (Table 2). This pattern of seasonal change in litter size is quite different from the pattern found in *M. montanus*, in which the peak in litter size occurs at the beginning of the breeding season, and is followed by a progressive decline. In this species, also, variations in natality are not the primary cause of the observed fluctuations in population density.

CORRELATIONS WITH PREVIOUS REPRODUCTION

It is possible to classify female *Microtus* as nulliparous, primiparous, or multiparous. Further, if a female is both pregnant and lactating, she has undergone post-partum breeding following the birth of the

litter she is now suckling. The criteria used to distinguish these different groups of females are presented below:

- I. No embryos, placental scars or mammary development
 - A. Small follicles presentimmature, nulliparous
 - B. Corpora lutea presentpuberal ovulation; non-pregnant or embryos unimplanted.
- II. Visible embryos
 - C. No mammary development or placental scarsprimiparous
 - D. Large mammae and/or placental scarsmultiparous
 1. Lactatingpost-partum breeding
 2. Not lactatingno post-partum breeding
- III. No visible embryos
 - E. Visible placental scars
 3. One set of scarsprimiparous
 4. More than one setmultiparous
 - F. Nipples large and prominent
 5. Lactatingsuckling litter
 6. Not lactating
 - (a) Uterus recently parturientlitter lost
 - (b) Uterus not recently parturientlitter lost or weaned

These criteria are considered quite reliable, with the exception of two—old placental scars and determination of lactation. Placental scars persist and the problem is to determine how many sets of scars are present. Two sets of scars can be readily discerned in some tracts, with occasional occurrence of a third.

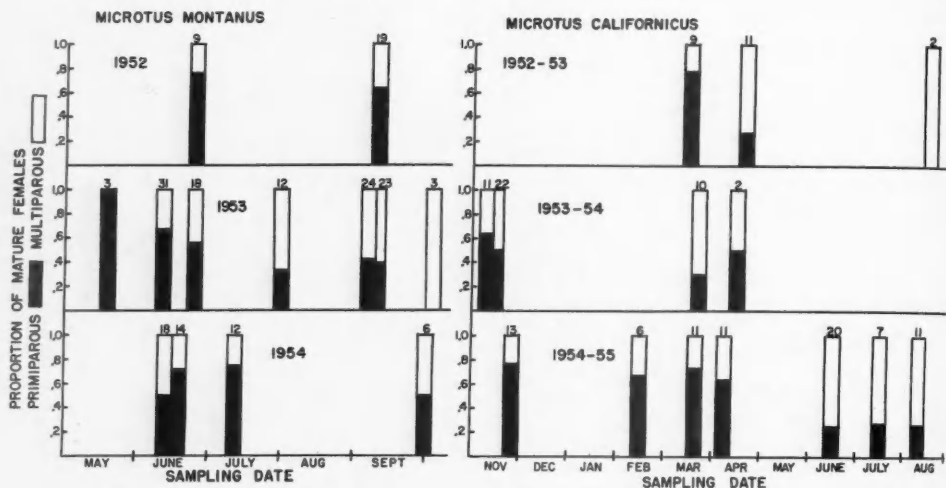
The criterion of lactation often used is the presence of milk in the nipples that can be expressed with forceps. This is conservative, in that there are some cases in which all appearances point to a lactating female and yet no milk can be expressed. To give one extreme instance, a female was snap-trapped while carrying an unweaned young in its mouth. Both were recovered immediately, and the dead female and living youngster were placed together in a box. The young vole was observed attempting to nurse for a period of several hours; however, no milk could be expressed from the nipples at any time. In such questionable cases, the females were considered to be lactating.

M. montanus. Mean corpora lutea, embryo, and placental scar numbers are shown in Table 3. There are no significant differences between primiparous and multiparous females in any of the counts, contrary to the situation in other species of *Microtus*. Neither is there any correlation between female weight and numbers of embryos or placental scars.

There is a regular seasonal progression in the relative numbers of primiparous and multiparous females in the catches (Fig. 2). A higher proportion of primiparous females would be expected early in the season, but the proportion would vary as breeding progressed depending on the relative rates of recruitment of immature females into the breeding population and mortality of mature females. In 1952 these two opposing forces were apparently closely balanced. In 1953, the multiparous females outnumbered primiparous for the last half of the season, suggesting that mortality of mature females was lower, since

TABLE 3. Ovulation rate and litter size in relation to previous reproductive history in *Microtus montanus*.

Females	MEAN NUMBERS								
	Corpora lutea			Embryos			Placental Scars		
	N	M	S. E.	N	M	S. E.	N	M	S. E.
Primiparous.....	118	6.68	± .18	64	6.35	± .22	41	6.22	± .24
Multiparous.....	76	6.69	± .22	45	6.55	± .31	59	6.02	± .18

FIG. 2. Seasonal changes in ratio of primiparous to multiparous females among mature female voles in trap catches. Sample sizes indicated above bars. Left, *Microtus montanus*. (September, 1954, sample from fertilized meadows.) Right, *Microtus californicus*.

survival of juveniles was also thought to be high at this time (see below). The data for 1954 indicate a reversal, and mortality among mature females presumably was higher than in the previous year. These differences may reflect changes in mortality associated with the vole cycle.

M. californicus. In contrast to *M. montanus*, multiparous females of *M. californicus* have larger litters than primiparous individuals. The mean embryo number for 36 primiparous females was $4.61 \pm .25$, and for 37 multiparous females, $5.19 \pm .34$. This difference is probably real, although not highly significant in these particular samples due to the presence of a single primiparous female with 8 embryos in the June, 1955, sample. Greenwald (1957:431) found a similar difference in embryo number, primiparous females averaging $3.91 \pm .18$ embryos, and multiparous, $4.45 \pm .16$.

The seasonal change in litter size noted above has been attributed to a larger proportion of older, multiparous females in the population at the height of breeding activity. The proportion of multiparous females in the population increases as the breeding season progresses, at least in some years (Fig. 2). These facts, however, are not the main reason for increased litter size in March and April, since both primiparous

and multiparous females have significantly larger litters in the March-April samples, taken at the height of the breeding season, than in the November samples, taken at the beginning of breeding activity (Table 4). (The June sample is deviant in that primiparous females averaged larger litters than multiparous females, but this is probably an artifact of small sample size.)

AGE OF REPRODUCTIVE MATURITY: FEMALES

The sooner members of a population reach sexual maturity and begin to breed, the more natality rate is accelerated. This is a possible mechanism for cyclic increase. Weight is here used as the age criterion, and in the case of pregnant females is corrected by subtracting the weight of the embryos.

M. montanus. Above a weight of 33 g, almost all females are reproductively mature, as evidenced by the presence of visible embryos, placental scars or corpora lutea (Table 5). This weight was constant for each of the three years studied. Below this weight, the number of breeding females was variable. In 1952 and 1953, the weight of the smallest breeding female was about 22-26 g in the spring, and 29-32 g in the autumn. In the spring of 1954, the smallest pregnant female was only 19.1 g, and 8 of 20 females be-

TABLE 4. Litter size in relation to previous reproductive history in *Microtus californicus*.

	PRIMIPAROUS					MULTIPAROUS		
	N	M	S. E.			N	M	S. E.
Combined November samples (embryos and new placental scars).....	15	2.73	± .18			15	3.60	± .16
Difference ± S. E. diff.....				.87	± .24			
Combined March and April samples (embryos only).....	22	5.14	± .25			20	6.60	± .41
Difference ± S. E. diff.....				1.46	± .48			
June sample (embryos only).....	3	5.33				9	3.56	

TABLE 5. Reproductive maturity in *Microtus montanus*. Figures in parentheses indicate numbers of individuals.

Mean sampling dates	FEMALES			MALES		
	% of females above 33 gm. weight that are mature	Weight of smallest mature female, gm.	% of mature females that are between 33 gms. and lowest mature weight	% of males above 35 gm. weight that are breeding	Weight of smallest breeding male, gm.	% of breeding males that are between 35 gms. and lowest breeding weight
1952						
June 24.....	100 (8)	21.5	100 (1)	100 (6)	30.5	100 (1)
Sept. 10.....	100 (17)	31.5	100 (2)	100 (10)	40.9	...
1953						
May 18.....	100 (2)	30.4	100 (1)	100 (14)	35.2	...
June 11.....	97 (31)	34.3	...	100 (26)	43.3	...
June 24.....	100 (12)	25.5	86 (7)	100 (10)	28.4	100 (6)
July 31.....	100 (11)	21.6	33 (3)	100 (16)	25.0	50 (6)
Sept. 6.....	100 (23)	31.7	100 (1)	100 (14)	41.4	...
Sept. 10.....	100 (22)	28.9	8 (13)	56 (9)	48.4	...
Oct. 4.....	100 (3)	33.7	...	no breeding		males
1954						
Apr. 30.....	no mat sample	ure fe	males in	100 (4)	38.6	...
June 12.....	100 (14)	19.1	40 (20)	96 (24)	26.7	33 (3)
June 18.....	100 (11)	23.6	100 (3)	100 (12)	26.7	54 (13)
July 11.....	100 (7)	29.9	100 (5)	100 (6)	28.9	100 (3)
Sept. 30 ¹	100 (6)	33.0	...	50 (2)	45.3	...

¹Sample from fertilized meadow.

tween 19.1 and 29 g had attained puberty. Although the difference is not large, the interpretation might be that overwintering female voles from the peak population of the preceding fall tended to begin breeding at a slightly earlier age. If this suggestion is correct, then the precocity occurring in a peak year did not defer significantly or prevent the decline that

followed. However, another possibility is that these females were underweight when they reached normal breeding age.

M. californicus. In females of this species, reproductive maturity during the height of the breeding season is attained around the weight of 25-30 g (Table 6). There seemed to be no great difference in any of the three years, but there is a marked seasonal change. During the non-breeding in the last half of the summer, most of the females are nulliparous, although they may weigh up to 35 g. With the onset of winter rains in November and the initiation of reproduction, these nulliparous females begin to breed, until in March all females above 25-30 g are mature. No extreme precocity was noted in any of the young females, as Greenwald (1956:220) reports.

AGE OF REPRODUCTIVE MATURITY: MALES

Macroscopic criteria of reproductive condition in males were employed, as suggested by Jameson (1950:435). This was unambiguous in almost all cases, but where there was some doubt, a smear of the epididymis always revealed an intermediate condition. In these, only small numbers of sperm were present, suggesting that the male was probably not capable of successful breeding.

M. montanus. Maturity is normally reached at a weight of about 35 g, and if growth rates are similar in both sexes, males and females reach maturity at about the same age (Table 5). Males were in breeding condition at the beginning of the female's breeding season, but no samples were available to indicate the commencement of reproductive activity. Mature males maintain this condition throughout the breeding season, and are joined by a variable number of precocious sub-adults in the late spring and summer, but these precocious males are not found toward the end of the season. The only possible difference in the whole series of samples is the decline in breeding activity in September, 1953, as compared with the previous year ($P = .10$). This, if real, may be due to the high density which the population attained at this time.

M. californicus. Sexual maturity in males during the height of the breeding season is reached at a weight of 35-40 g, or about 10 g heavier than the

females, in contrast to the montane vole (Table 6). There is seasonal variation in attainment of maturity in males as well as females. During the late estival pause in breeding, no males are in breeding condition. With resumption of breeding activity following the first winter rains, those males well above 40 g come into breeding condition first. As the season continues, the smaller males also become reproductively active. There were no noticeable differences in this pattern between any of the three years.

The breeding season in *Microtus californicus* is much less sharply defined (Greenwald 1957:426) than in *M. montanus*. Because of the more gradual onset and waning of seasonal breeding activity, comparisons between the two species are difficult. In *M. californicus*, females may mature more quickly, and males more slowly, than in *M. montanus*, but this is true only if the growth rates of the two species are similar, since weight was the age criterion adopted. In both species, however, no change in rapidity of maturation was noted during the course of the population cycle.

THE BREEDING SEASON

Another means by which natality might be increased is for the number of litters produced during the breeding season to be increased. This would be accomplished if the breeding season were lengthened, the interval between successive pregnancies in an individual shortened, or the proportion of pregnant females in the population increased.

M. montanus. The length and timing of breeding for the three years studied are given in Fig. 3. The breeding season was determined by calculating the breeding date which would have produced the oldest juvenile in the early spring catches, and the birth date of the smallest embryo present in the late fall catches. Weight was the age criterion employed for both embryos and juveniles. Although it is realized that sample size will affect such a calculation, there seems to be a remarkable constancy for the whole period. The 1954 season is only slightly longer than that of 1952, and the onset of breeding is identical in 1952 and 1953. In 1954, breeding commenced two weeks earlier; this may be related to the peak population of the previous fall, or to some difference in spring weather in 1954.

Table 7 and Fig. 3 show the percentage of mature females in the sample that are pregnant, or prevalence of pregnancy (Davis, 1953:385), in the different seasons and years. The method suggested by Davis & Zippen (1954:171) was used to compare the samples statistically. The percentage of pregnant females in spring and fall of 1952 remained essentially the same. Prevalence in June, 1953, was at least as great as the previous year, then fell off as summer continued, and by September, 1953, was significantly lower than in September, 1952 ($P < .002$). This may be another manifestation of the inversely response to the high population level in the autumn of 1953. The prevalence of pregnancy in June of 1954 was markedly lower than in the two previous springs

TABLE 6. Reproductive maturity in *Microtus californicus*. Figures in parentheses indicate numbers of individuals.

Mean sampling dates	FEMALES			MALES		
	% of females above 40 gm. weight that are mature	Weight of smallest mature female, gm.	% of mature females that are between 30 gm. and lowest mature weight	% of males above 40 gm. weight that are breeding	Weight of smallest breeding male, gm.	% of breeding males that are between 40 gm. and lowest breeding weight
1953						
Mar. 16.....	100 (9)	25.0	100 (3)	100 (6)	48.5	...
Apr. 21.....	100 (11)	28.5	100 (1)	100 (1)	36.2	100 (1)
Aug. 17.....	33 (6)	42.3	...	No breeding		males
Nov. 10, 15.....	79 (42)	29.0	33 (6)	44 (25)	51.4	...
1954						
Mar. 21.....	100 (9)	28.0	100 (1)	100 (5)	46.5	...
Apr. 14.....	100 (2)	32.8	...	100 (5)	36.7	100 (1)
Nov. 25.....	93 (14)	32.9	...	67 (6)	45.4	...
1955						
Feb. 14.....	84 (6)	25.5	100 (1)	100 (10)	37.5	100 (1)
Mar. 19.....	100 (11)	35.9	...	100 (11)	47.7	...
Apr. 7.....	100 (9)	26.9	100 (2)	100 (9)	38.4	100 (3)
May 12.....	100 (3)	23.4	100 (1)	100 (4)	42.0	...
June 15.....	77 (26)	30.5	...	50 (2)	33.4	100 (1)
July 14.....	100 (7)	31.1	...	33 (3)	38.4	80 (2)
Aug. 10.....	69 (16)	32.4	...	no breeding		males

($P < .002$), and might reflect either the high population density preceding the period, or the decline soon to follow. During the time of rapid population decline, in July, 1954, there is some indication that prevalence of pregnancy increased ($P = .09$); again this could be interpreted as inversely related to density.

M. californicus. The absence of a sharply defined beginning and end in the reproductive activity of *M. californicus* makes difficult the calculation of length and timing of the breeding season in each year. In nature, some breeding probably occurs in every month of the year with the major breeding effort in late winter and spring, and a minor peak in the fall (Greenwald 1956:213). Reproductive activity during the winter is variable, and may depend on the temperature. The prolongation of major breeding into the summer is also variable, and may depend on the amount and duration of the spring rains that provide green vegetation (Greenwald 1957:423).

In practice, it was necessary to calculate the apparent breeding season from the samples available in the same manner as was done for *M. montanus*, so

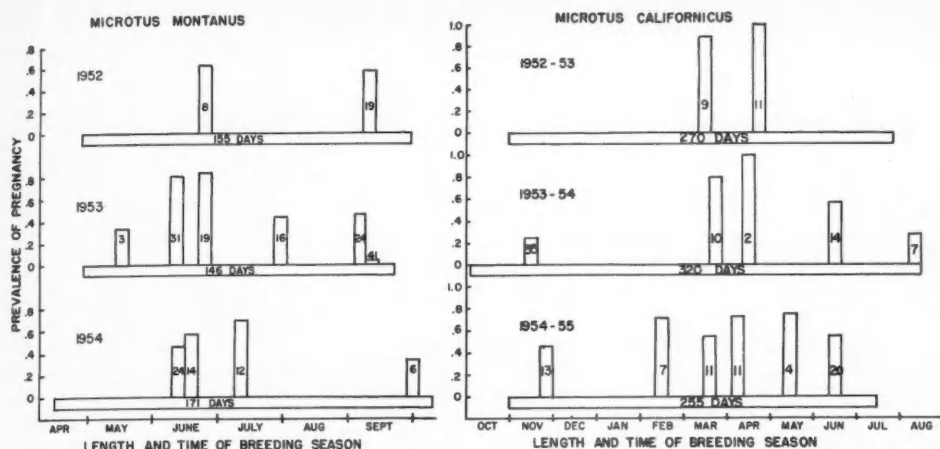


FIG. 3. Length and timing of breeding season, and prevalence of pregnancy, in vole populations. Sample sizes indicated within bars. See text for explanation of calculations. Left, *Microtus montanus*. (September, 1954, sample from fertilized meadow.) Right, *Microtus californicus*.

TABLE 7. Seasonal and year-to-year variation in prevalence of pregnancy in mature females of *Microtus montanus*.

	1952		May 18	1953					1954			
	June 24	Sept. 10		June 11 24	July 31	Sept. 6 10	June 12 18		July 11	Sept. ² 30		
Number of adults.....	8	19	3	31	12	8	24	22	14	11	7	6
Number pregnant.....	5	11	1	25	11 ¹	3	11 ¹	0	7	5	4	2
Number of sub-adults.....	7	8	19	10	3	5
Number pregnant.....	5	4	1	4	3	5
Prevalence of pregnancy.....	.625	.579	.333	.807	.842	.437	.458	.024	.458	.571	.750	.333
	.592			.458					.536			

¹Includes one pregnant female with all embryos resorbing.

²Sample from fertilized meadow.

that some sporadic activity may not be included. The length and timing of the breeding season for the study period is presented in Fig. 3. The date of first breeding in November, 1952, is hypothetical, and based on similarity in population structure between the samples in March, 1953, and March, 1955. If anything, breeding in 1952 probably began later than the first of November. The breeding season in 1953-54 was lengthened at both ends over the preceding year, and this led to a minor population peak in the summer of 1954. Following the summer, breeding resumed around the first of November and reached a high level throughout the spring of 1955. Breeding tapered off in June, at which time population density reached a major peak, and the last young were probably born in mid-July, 1955.

Prevalence of pregnancy during the three years is shown in Table 8 and Fig. 3. The proportion of pregnant females is moderate at the beginning of the breeding season, builds up to a high level and then declines toward the end of the season. Prevalence in the combined March-April samples is the same in 1953 and 1954, but in 1955 it is significantly lower ($P < .009$). Prevalence of pregnancy continued to

drop in June, 1955, as population density attained a peak. In *M. californicus*, as in *M. montanus*, pregnancy rate during the height of the breeding season seems to be inversely related to population density, as witnessed by the decline in this rate in the March-June samples from 1953 to 1955, during which time progressively higher densities occurred at the close of successive breeding seasons.

The difference between the November samples in 1953 and 1954 may be due to the fact that the 1954 sample was taken ten days later than the one in 1953. However, if the difference in time of sampling was not critical, such a difference in pregnancy rate might be a consequence of the above-mentioned inversely relationship, since vole numbers were apparently quite a bit higher in the fall of 1953 than in the next year (Fig. 1).

LITTER PRODUCTION

If, first, the duration of the breeding season is determined, and then the prevalence of pregnancy occurring at intervals during its course, it is possible to calculate the rate of litter production in each of the three years, using the formula given by Emlen &

TABLE 8. Seasonal and year-to-year variation in prevalence of pregnancy in mature females of *Microtus californicus*.

	1953			1953-54				1954-55							
	Mar. 16	Apr. 21	Aug. 17	Nov. 10, 15	Mar. 21	Apr. 14	June 16 ¹	Aug. 11 ¹	Nov. 25	Feb. 14	Mar. 19	Apr. 7	May 12	June 15	July 14 Aug. 10
Number of mature females.	9	11	3	35	10	2	14	7	13	7	11	11	4	20	18
Number pregnant....	8	11	0	8	8	2	8	2	6	5	6	8 ²	3	11	0
Prevalence of pregnancy..	.889	1.00	0.0	.229	.800	1.00	.571	.286	.461	.715	.545	.727	.750	.550	0.0
	.950				.833						.636				

¹Data from S. F. Cook, Jr.; specimens not seen.²Includes one pregnant female with all embryos resorbing.

Davis (1948:63). In making the calculations, the different pregnancy rates were prorated among those portions of each breeding season of which they were representative, and the number of days in gestation in which embryos can be seen was taken to be 16 days. This is derived from Fig. 4, in which embryo length *in utero* is plotted against weight of embryos plus reproductive tract divided by the number of embryos.

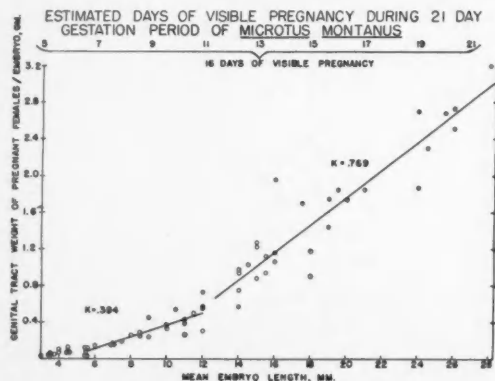


FIG. 4. Weight-length relationship in *Microtus montanus* embryos used to estimate number of days during gestation period when female is visibly pregnant. Data are plotted on arithmetic coordinates for direct comparison with Fig. 2 in Emlen & Davis (1948). A semi-log plot indicates change in rate of embryo growth at about 12-13 mm. mean embryo length.

This gives a measure of the weight-length relationship in the developing embryo. Embryos 27 mm long are considered full term, as this is the mean upper limit of fetal size observed, and embryo weight corresponds to observed weight of newborn voles (Greenwald 1957:428; Hatfield 1935:268). The sharp change in slope of the weight-length curve about day 11 of gestation seems to correspond to a similar change noted by Emlen & Davis (*loc. cit.*) in developing embryos of albino rats (*Rattus norvegicus*) between days 11 and 12 of a 22-day gestation. The embryos of the albino rat become visible on dissection on the seventh day of gestation and it is assumed that

those of *Microtus* become visible slightly sooner, about the sixth day. The similarity between the rat and vole curves is so great that the error of this assumption is probably no greater than ± 0.5 days.

M. montanus. Based on this method of calculation, litter production in the montane vole was: in 1952—5.15; in 1953—4.71; and in 1954—4.38. There is a fairly even decrease in number of litters over the three-year period. In both intervals (1952-53; 1953-54), the decline in litter production is directly related to shortening of the breeding season and lower overall pregnancy rates. There is no evidence that an increase in litter production caused the vole population to build up to a peak in 1953, or conversely, that decreased litter production was the major cause of the crash decline in 1954, although it could have played a contributing role. Litter production in *Microtus montanus* is primarily controlled by prevalence of pregnancy, which, as noted above, bears in general an inverse relationship to population density.

Theoretical litter production, assuming either universal post-partum breeding, or no post-partum breeding, gives a standard of comparison for the estimations of actual litter production. With universal post-partum breeding, length of the breeding season divided by length of gestation equals the theoretical maximum litter production. These were: in 1952—7.39; in 1953—6.96; and in 1954—6.71. With no post-partum breeding, an arbitrary interval of 42 days (21 days gestation, 14 days lactation, and 7 days between weaning and remating), as used by Greenwald (1957:443), is assumed. Theoretical maximum litter production is then: in 1952—3.69; in 1953—3.48; and in 1954—3.40.

The estimated litter production falls between the two theoretical figures in all three years, and bears almost the same relation to them in each year. This agrees with the observation that post-partum breeding is not universal in the population and does not vary much (see below).

M. californicus. Calculated litter production in this species was: in 1952-53—10.56; in 1953-54—11.22; and in 1954-55—9.30. Theoretical maximum litter production, assuming universal post-partum breeding,

is: in 1952-53—12.75; in 1953-54—15.20; and in 1954-55—12.20. If no post-partum breeding is assumed, the theoretical values are: in 1952-53—6.37; in 1953-54—7.60; and in 1954-55—6.10. The calculated number of litters produced falls in between the theoretical extremes that could be produced with universal and with no post-partum breeding. In 1952-53, the population more closely approached the theoretical maximum than was the case in 1953-54 or 1954-55, but the difference is not great.

The increased production in 1953-54 is apparently a result of the longer breeding period, rather than any change in proportion of breeding females in the population. These findings are contrary to what was found in *M. montanus*, in which there was little change in length of breeding season and litter production during the course of the population cycle. Thus, in *M. californicus*, but not *M. montanus*, a more prolonged breeding season may be followed by a higher population density. Greenwald (1957:434-35) also found this to be the case in his study of *M. californicus*. However, this is not invariable, as is attested by the peak population density produced in the short breeding season of 1954-55. The lower litter production during this year seems due to both a shorter season and reduced prevalence of pregnancy.

POST-PARTUM BREEDING

M. montanus. The percentages of females which could definitely be classed as post-partum breeders, being both pregnant and lactating, are shown in Table 9. The range of variation is small, and the average for only those samples in which some post-partum breeders were found is 17.6%. No post-partum breeders were found in 3 out of the 10 samples (excluding May, 1953), and the over-all average rate is hence reduced to 11.7%. Since the two criteria of post-partum breeding (visible pregnancy and lactation) coexist simultaneously for only about half of the post-partum gestation, the prevalence of post-partum breeding is probably closer to 24% in the population. This agrees only roughly with the position of litter production between the theoretical litter numbers calculated by assuming universal, or no, post-partum breeding. The amount of post-partum breeding which would account for the differences between actual litter production and production with no post-partum breeding is, in %, 50 in 1952, 35 in 1953, and 29 in 1954. These figures are considerably greater than the observed prevalence of post-partum breeding.

M. californicus. The average prevalence of post-partum breeding, in those samples in which any is found, is 18.8%, and the range of seasonal and year-to-year variation is not great (Table 9). If the four samples containing no post-partum breeders are included, the rate is reduced to 14.9%. But since a post-partum breeding female is recognizable for only about half of the post-partum gestation, the actual prevalence of post-partum breeding is probably about 30%, nearly the same as in *M. montanus*.

TABLE 9. Prevalence of post-partum breeding in voles.

<i>Microtus montanus</i>	NUMBER OF FEMALES				A-B; % of post-partum breeders among breeding females
	Pregnant	Lactating	Both Pregnant and Lactating, A	Breeding, B	
1952					
June 24.....	5	5	2	8	25
Sept. 10.....	11	8	0	19	0
1953					
May 18.....	1	0	0	1	0
June 11.....	25	2	0	27	0
24.....	15	3	3	15	20
July 31.....	7	6	1	12	8
Sept. 6.....	10	14	4	23	17
10.....	1	7	0	8	0
1954					
June 12.....	11	10	4	18	22
18.....	8	9	3	14	21
July 11.....	9	3	1	12	8
Sept. 30 ¹	2	5	1	6	17
<i>Microtus californicus</i>					
1953					
Mar. 16.....	8	2	1	9	11
Apr. 21.....	11	2	2	11	18
Aug. 17.....	0	0	0	0	0
1953-54					
Nov. 15.....	8	10	3	18	17
Mar. 21.....	8	4	3	10	30
Apr. 14.....	2	0	0	2	0
1954-55					
Nov. 25.....	6	2	0	8	0
Feb. 14.....	5	2	1	6	17
Mar. 19.....	6	3	0	9	0
Apr. 7.....	7	4	2	10	20
May 12.....	3	1	1	4	25
June 15 ²	11	0	3	17	18

¹Sample from fertilized meadow.

²No pregnant or lactating females in July and August samples.

When this figure is compared with the calculated prevalence of post-partum breeding necessary to account for the difference between actual litter production and theoretical production with no post-partum breeding, it is seen that the latter rate is about twice as great as the observed post-partum breeding, being 66% for the 1952-53 breeding season, 48% for the 1953-54 season, and 52% for the 1954-55 season.

Several possible sources of error might cause these discrepancies, observed in both species. The most probable is failure to recognize lactating females, which leads to underestimation of observed prevalence of post-partum breeding. Another possibility is that the calculated litter production is too high, because of inadequacy of the samples on which it is based.

SUMMARY OF REPRODUCTION

It is clear that no constant and direct causal relationship between natality and population cycles exists in either *Microtus montanus* or *M. californicus*. Ovulation rate and litter size, the expressions of natality, tend to vary inversely with population density and thus to run counter to the cyclic trend of the population, except during the crash decline period in *M. montanus*, when lowered litter size may contribute to the drop in density. (No reproductive data from the crash decline in *M. californicus* in 1955-56 are avail-

able). Other factors influencing natality either vary inversely with density (prevalence of pregnancy), or show no significant year-to-year variation (age of maturity, incidence of post-partum breeding).

Length of the breeding season exhibits only slight variation in *M. montanus*. The main difference between the two species lies in the greater variability in length of the breeding season, and consequent variable litter production, that is found in *M. californicus*. While a direct relationship between litter production and cyclic increase may contribute to some periodic increases in population density, this relationship is not obligate, as the data for 1955 demonstrate.

These considerations lead to the conclusion that the immediate cause of population cycles in these species must lie within the other half of the natality-mortality equation.

MORTALITY

Variations from year to year in mortality could result in fluctuations in density of a population. Variable mortality might occur at any developmental stage, from the time of ovulation on. For this reason both prenatal and postnatal mortality must be considered as possibly contributing to cyclic mortality.

Variable prenatal mortality would produce fluctuations in litter size, unless increased mortality were balanced by an increased ovulation rate. As previously noted, both ovulation rate and litter size in general varied inversely with population density; however, continued low natality rate during the period of population decline might be due to increased prenatal loss. Determination of prenatal mortality rates provides a check on the conclusions concerning natality.

Prenatal mortality has been most adequately discussed by Brambell (1948) who stresses the importance of the distinction between pre-implantation and post-implantation mortality. He concluded that, in the wild rabbit (*Oryctolagus cuniculus*), mortality before implantation of the embryos was independent of that occurring after and should be treated separately.

PRE-IMPLANTATION MORTALITY

Pre-implantation loss may be considered as the difference between the number of corpora lutea in the ovaries of pregnant females, and the number of implantation sites in the uteri. However, this loss does not include litters ovulated, all of which failed to implant, since with the loss of all ova, no implantation sites and no embryos would develop, and the female would not be classed as pregnant. Brambell & Mills (1947:201) determined the extent of whole litter loss by perfusing uterine tracts, and recovering ova and unimplanted embryos. They concluded that the loss of whole litters before implantation was between 1.00 and 3.64%. In the present study, no perfusion was carried out on either species of *Microtus* and the extent of this type of mortality cannot be determined. A comparison of the number of *M. montanus* females with corpora lutea and no visible implantation sites (19) with the expected number (29) of pregnant females with non-visible embryos (num-

ber of pregnant females $\times 5/16$) gives some indication that in this vole population, too, the number of whole litters lost prior to implantation is insignificant.

These data on corpora lutea and implantation sites are subject to several types of error. Corpora lutea counts may not be perfectly reliable, as discussed previously. A second error would be introduced if, following the death of an embryo, the implantation site rapidly disappeared. Conaway (1955:529-531) found that implantation sites (placental scars) are formed and persist in the laboratory rat when embryo death occurs as early as the seventh or eighth day of pregnancy, so long as some of the embryos remain alive past the eleventh day of pregnancy. Brambell, Henderson & Mills (1948:217) determined that under similar circumstances implantation sites persist until parturition in the rabbit, but their data also indicated a significant change in the mean number of implantation sites during the course of gestation. When the gestation period subsequent to the tenth day was divided into four equal parts, a significant rise was noted in implantation site counts between the first and second quarters, and a significant drop between the third and last quarters (Allen, Brambell & Mills 1947:326). The terminal decline could be explained by the disappearance of about 9% of the implantation sites, but in view of the experimental evidence of persistence of the sites, this is not a sure explanation. They conclude: "The significant decline in the mean number of implantation sites towards the end of gestation may be due to an experimental error arising from disappearance of sites, or failure to count them, but there may be some other explanation" (Brambell & Mills 1948:241).

A similar pattern is seen in the data for *Microtus montanus* (Table 10). Between the first and middle thirds of the visible pregnancy period, there is a slight rise in the mean number of implantation sites, which is not statistically significant. Between the middle and last thirds there is a significant ($P = .01$) drop in the mean number, amounting to 15.7%. The most plausible explanation would seem to be failure to count sites obscured by the large embryos of the last part of gestation. Even so, the number of such late-stage pregnancies is small, and the apparent disappearance of sites hence would not greatly influence the estimation of pre-implantation mortality.

In *Microtus californicus*, the change in mean number of implantation sites follows a pattern contrary to that just discussed. The data presented in Table 10 indicate a decline in number of implantation sites between the first and middle thirds of pregnancy, and an increase between the middle and last thirds. None of these changes are, however, significant.

A third source of error derives from the fact that in some females of *M. montanus* the number of implantation sites in the uteri exceeds the number of corpora lutea in the ovaries. Polyovuly and/or polyembryony might produce such a disparity. The situation was also found in the rabbit (Allen, Brambell & Mills 1947:324) and in the Norway rat (Davis &

TABLE 10. Changes in mean number of implantation sites per female vole during gestation.

<i>Microtus montanus</i>	STAGE OF PREGNANCY IN DAYS						
	5 10			11-15		16-21	
	M	S. E.		M	S. E.	M	S. E.
Mean number of implantation sites.....	6.84	± .23		7.12	± .30		6.00 ± .34
Difference ± S. E. diff.....			+ .28 ± .37			-1.12 ± .45	
Sample Size.....	55			34		17	
<i>Microtus californicus</i>							
Mean number of implantation sites.....	5.02	± .30		4.63	± .38		5.60 ± .48
Difference ± S. E. diff.....			- .39 ± .48			+ .97 ± .61	
Sample Size.....	44			19		19	

Hall 1950: 189), where it was assumed polyovuly was responsible because of the absence of twins in a common chorion. No synchronic twins have been identified in either species of *Microtus*, and polyovuly is tentatively advanced as the explanation in this case also.

Hartman (1926) reviewed the occurrence of polyovular follicles in mammals, and concluded that rarely, if ever, did such follicles produce viable ova (*op. cit.*:29). However, in the rabbit and Norway rat, considered above, the investigators believed that polyovular follicles might give rise to more than one individual. Whereas the percentage of litters in which polyovuly occurred in the rabbit was only 1.32% (Allen, Brambell & Mills, *loc. cit.*), in *Microtus* it is calculated as at least 11.9% (14/108; see Table 11). This figure does not include cases in which polyovuly is masked by pre-implantation mortality in the same individual, thus producing no apparent discrepancy between the number of corpora lutea and implantation sites.

TABLE 11. Polyovuly and pre-implantation mortality in *Microtus montanus*.

	NUMBER OF IMPLANTATION SITES						
	Greater than number of corpora lutea		Equal to number of corpora lutea	Less than number of corpora lutea			
	+2	+1	0	-1	-2	-3	-4 -5
Number of pregnant females.....	2	12	61	17	9	4	2 1
Total sample, 108.....	14 Cases of polyovuly		Cases of polyovuly plus pre-implantation loss, or neither	33 Cases of pre-implantation loss			

Davis & Hall (*loc. cit.*) found more embryos than corpora lutea in 21% of the pregnant wild rats that they examined, almost twice the uncorrected incidence (11.9%) observed in *M. montanus*. Here the occurrence of polyovuly was confirmed by the presence of recognizable polyovular follicles in 12% of the rats.

From the foregoing, it may be concluded that the only error of any magnitude introduced into the calculation of pre-implantation mortality from the difference between the number of corpora lutea in the ovaries of pregnant females and the number of implantation sites in the uterine horns is that error resulting from polyovular follicles producing more than one viable ovum.

M. montanus. Table 12 gives the seasonal and yearly variation in pre-implantation mortality, not including loss of whole litters and not corrected for polyovuly. Although the sample sizes are too small to permit definite conclusions, several trends are consistent. Mortality is lower in the spring than in the fall in all years. Combining all June and all September samples, the pre-implantation mortality in June is 4.55%, and in September, 12.55%. Spring mortality shows a progressive increase, albeit a slight one, throughout the study period.

When all samples are combined, overall pre-implantation loss is 5.86%. For the wild rabbit, Brambell (1948:391) cites a loss of 10.2 to 13.0% during this phase.

Pre-implantation mortality was lower in the fall of 1953, when the population peaked, than it was in September of either the preceding or following year, and this may possibly reflect a cyclic influence. However, mortality at this stage of life is not of sufficient magnitude to account wholly for the observed population fluctuation.

M. californicus. Pre-implantation mortality in *Microtus californicus* cannot be estimated, because of the occurrence of accessory corpora lutea (see above, Ovulation Rate). Also, the occurrence of polyovuly is uncertain. In no case were there more embryos than corresponding corpora lutea, but in three individuals there were one or two more new placental scars than corpora. This suggests that polyovuly may occur at least occasionally, and agrees in part with Greenwald's (1956:220; 1957:432) findings.

POST-IMPLANTATION MORTALITY

Post-implantation mortality may be considered as the difference between the number of implantation

TABLE 12. Prenatal mortality in *Microtus montanus*.

Mean number and S. E.	1952		1953			1954		
	June	Sept.	June	July	Sept.	June	July	Sept.
Corpora lutea of pregnant females, A...	8.40 ± .25	6.73 ± .30	7.76 ± .21	6.71 ± .36	4.50 ± .23	8.10 ± .27	6.00 ± .53	4.00 ± 1.0
Implantation sites of pregnant females, B	8.20 ± .20	5.64 ± .36	7.47 ± .19	6.71 ± .42	4.17 ± .30	7.58 ± .34	5.56 ± .41	3.00
A-B=pre-implantation loss.....	.20 2.4%	1.09 16.2%	.32 4.1%	0.033 7.3%	.52 6.4%	.44 7.3%	1.00 25%
Living embryos, C.....	7.80 ± .49	5.45 ± .43	7.16 ± .22	6.57 ± .37	4.09 ± .28	7.42 ± .34	5.22 ± .40	3.00
B-C=post-implantation loss.....	.40 4.9%	.19 3.4%	.31 4.2%	.14 2.1%	.08 1.9%	.16 2.1%	.34 6.1%	0.0
A-C=over-all prenatal mortality.....	.60 7.1%	1.29 19.0%	.60 7.7%	.14 2.1%	.41 9.1%	.68 8.4%	.78 13.0%	1.00 25%
Sample size.....	5	11	45 ¹	7	12 ¹	19	9	2

¹Includes one pregnant female with all embryos resorbing.

sites and the number of living embryos in the same pregnant females. Not included are cases in which the entire litter dies soon after implantation and resorption or abortion proceeds rapidly, so that the female is eliminated from the class of pregnant females. The measurement of post-implantation loss of individual embryos is subject to a possible source of error already discussed, that is, gradual disappearance of the embryo and implantation site after the embryo's death. Such disappearance is probably very rare (see Conaway *loc. cit.*).

M. montanus. Seasonal and yearly changes in apparent post-implantation mortality are shown in Table 12. Again, sample sizes are small, but certain trends are apparent. Mortality is higher in the spring than in the fall in all years. Post-implantation mortality in the combined June samples is 3.89% and in the combined September samples, 2.63%. Spring mortality consistently decreases during the three years.

A reciprocity thus seems to exist between pre- and post-implantation loss in these samples. As pre-implantation loss increases, post-implantation loss decreases. However, this relationship is not borne out by the mid-summer sample of 1953, in which there was no pre-implantation loss, but in which post-implantation loss was very low.

It should be remembered that the estimates of post-implantation mortality derived above are influenced by the nature of the sample. The females trapped are in all stages of gestation, and the embryos are still in the process of suffering post-implantation losses. Thus, the above estimate is minimal because the loss is incomplete. Actual post-implantation loss in *M. montanus* may be double the calculated spring and fall mortality. The magnitude of the actual loss is suggested by comparing litter size in the middle and last thirds of visible pregnancy. In the combined

June samples, number of normal embryos declines from 7.41/♀ for those in the middle third of pregnancy to 6.67/♀ for those in the last third, a loss of 10.0%. In the July and September samples, litter size decreases from 5.41/♀ to 5.18/♀, or a drop of 4.25%. Unfortunately, sample size is too small to test the significance of the difference, but the figures are reasonable. Ranson (1941:48) found a post-implantation mortality (resorption) rate of less than 10% in laboratory *Microtus agrestis*.

Brambell (1948:385) has a good discussion of the problems inherent in the estimation of the loss of whole litters after implantation, and presents several possible methods. One method is to compare the relative frequency with which females in early, middle, and late stages of pregnancy are obtained. If there is a decrease in numbers caught in the later stages, this might indicate an early loss of the whole litter, abortion or rapid reabsorption of the embryos, and the disappearance of the female from the class of pregnant females. The objection to this is that there may be bias in the sampling method which favors females in one stage of pregnancy over those in another. There is some evidence for the white rat that the activity of the female decreases as gestation progresses (Wang 1923:20). In addition, Becker (1954:120) found that wild *Rattus norvegicus* females were more easily trapped in the first half of pregnancy than in the last half. This might account for the decrease in catch of females in advanced stages of pregnancy. However, Brambell (1948:395) employed this method and arrived at a loss of 35.5% of litters as units, which is very close to the estimate he obtained by another method.

Fewer pregnant voles were caught in middle and late stages of pregnancy than in early stages (Table 13). This decline was greatest in the early part of the season, since not all the pregnant females had yet

had time to progress to the later stages. Later in the breeding season, the proportion of middle and late pregnancies was much greater because the approach of the end of breeding stopped the recruitment of newly pregnant females into the population. The over-all average indicates a "loss" of 69 % of litters as units. This seems extremely high, being twice the loss found in wild rabbits, and the estimate is not considered reliable. Loss of entire litters may be considerable after implantation, but the data from this *Microtus* population are not adequate to determine its extent. There is no indication that increased post-implantation loss of whole litters occurred during the population decline. Such loss would produce a decline in prevalence of pregnancy, and this did not occur.

TABLE 13. Numbers of female voles caught at different stages of gestation.

	STAGE OF PREGNANCY IN DAYS			
	5-10	11-15	16-21	
<i>Microtus montanus</i>				
Number of pregnant females caught.....	40	22	6	June samples
Difference; per cent "loss".....	18 45%	16 73%		
Number of pregnant females caught.....	15	12	11	July, Sept. samples
Difference; per cent "loss".....	3 20%	1 8%		
<i>Microtus californicus</i>				
Number of pregnant females caught.....	31	14	9	March-June samples
Difference; per cent "loss".....	17 55%	5 36%		
Number of pregnant females caught.....	13	5	1	Nov.-Feb. samples
Difference; per cent "loss".....	8 62%	4 90%		

M. californicus. Seasonal and year-to-year changes in apparent post-implantation mortality are shown in Table 14. Little variation exists, and no definite pattern in the occurrence of resorbing embryos can be found in a sample of this size. Overall rate of loss is 14 resorbing embryos out of 357 or 3.92%. This rate is slightly lower than the 5.16% overall post-implantation loss in *M. montanus*. The estimate is minimal, however, because post-implantation loss is still incomplete. A check on the estimated loss derived from the difference in mean litter size between the various stages of pregnancy shows that between the first and middle thirds of visible pregnancy, mean embryo number declines by 8.35%. Between the middle and last third of visible pregnancy, there is a

6.3% decline in the mean embryo count in the November-February samples, and a 5.2% increase in the March-April samples. Small sample size makes these estimates uncertain, but post-implantation loss of individual embryos is probably on the order of 5-10%, the same as in *M. montanus*.

The proportions of females in early and middle stages of pregnancy is the same both early in and at the height of the breeding season, and the decline between the two stages is 57% (Table 13). Fewer females in the last third of visible pregnancy were found in the November-February samples than in the March-June, as would be expected. The overall decline in catch of pregnant females was 77%. This is much too high to be accounted for by post-implantation loss of whole litters, and is probably due largely to a decline in the activity, and thus trappability, of females in later stages of pregnancy (see above).

Insofar as they can be compared, both *M. californicus* and *M. montanus* have similar rates of prenatal loss. But while no clear pattern of prenatal mortality is found in the data for *M. californicus*, several patterns may be tentatively identified in *M. montanus*. One of these is the reciprocal relationship that seems to exist between pre- and post-implantation losses. Another is the relationship with population density. Overall prenatal mortality, including both pre- and post-implantation components, is lowest in the July and September samples of 1953, when the population reached a peak, and is highest in the July and September samples of 1954, when the population crashed (Table 12). That this relationship between prenatal mortality and the population cycle is not fully reflected in a similar natality relationship (see above) is due to the greater magnitude of the inverse relationship between ovulation rate and population density which overrides the influence of prenatal mortality during the period of population increase. During the "crash" decline, lowered litter size results from heightened prenatal mortality. However, the magnitude of the drop in litter size is not sufficient to account for the associated population "crash," and the major cause of changes in density must lie in postnatal mortality rates. The postnatal period can be broken down into nestling, juvenile, and post-juvenile stages.

PARTURITION AND NESTLING MORTALITY

A possible indication of the magnitude of early mortality in young voles in the nest is a comparison of the number of placental scars in recently parturient females with the number of prominent mammae in females in the same sample. Mammae are thought to become prominent, i.e. the hair of the female is worn away from around them, through the suckling of the young, so the number of prominent or "active" mammae may be an indicator of the number of young that are suckling at the time the female was caught.

Two distinct kinds of mortality may befall nestling voles. The first will befall whole litters as units, due to the finding of a nest by a predator, or the death of the mother before the young are old enough to sur-

TABLE 14. Prenatal mortality in *Microtus californicus*

Mean number and S. E.	1953			1954			1955			
	Mar.	Apr.	Nov.	Mar.	Apr.	Nov.	Feb.	Mar.	Apr.	June
Implantation sites of pregnant females, A...	6.0 ± .63	6.90 ± .64	3.25 ± .23	5.38 ± .50	6.00	3.17 ± .17	4.40 ± .26	5.50 ± .56	6.44 ± .40	4.00 ± .50
Living embryos, B.....	6.0 ± .63	6.40 ± .76	3.13 ± .29	5.38 ± .50	6.00	3.00 ± .26	4.40 ± .26	5.33 ± .71	5.71 ± .29	3.91 ± .55
A - B = post-implantation loss.....	0.0	0.5 7.3%	.12 3.7%	0.0	0.0	.17 5.4%	0.017 3.1%	.73 11.3%	.09 2.3%
Sample size.....	8	11	8	8	2	6	5	6	8 ¹	11

¹Includes one pregnant female with all embryos resorbing.

vive alone. The second type is the occurrence of individual deaths among the young of a litter, due to inherent weakness or disease in some of the young. Losses of the second type could reasonably be expected to have a normal distribution, whereas the first would not. This may be the reason for the shape of the frequency polygon of numbers of "active" mammae (Fig. 5). If nursing young voles indiscriminately suckled at all of their mother's nipples, all nipples of any lactating female would be equally prominent. This is not the case, and suggests that the number of prominent nipples in a lactating female may be a function of the number of young recently suckled.

FREQUENCY DISTRIBUTION OF "ACTIVE" MAMMAE IN *MICROTUS MONTANUS*

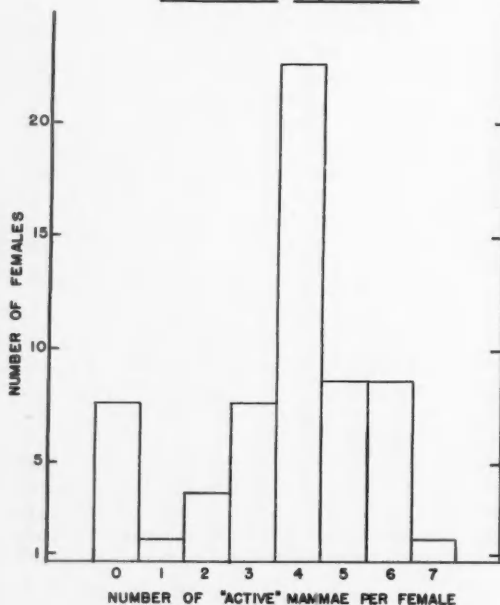


Fig. 5. Frequency distribution of "active" (i.e. prominent) mammae in *Microtus montanus*. See text for explanation.

The large zero class in the frequency polygon (nipples large, but not prominent, in recently parturient females) might be ascribed to whole litter loss. Because of this, the zero class has been eliminated from calculation of the standard error of the mean number of active mammae (Table 15). The loss of whole litters is probably more frequent than is apparent, because litter loss due to maternal death is not included.

M. montanus. Seasonal and yearly values for mean numbers of placental scars and "active" mammae are given in Table 15. Unfortunately, mammae were not recorded in 1952. With one exception, the variation from year to year is not large enough to be significant, and the average difference between placental scar and active mammae number for all samples is 37.8%, which may be considered a rough measure of parturition and nestling mortality in these voles. Two possible sources of error in this calculation are of opposite sign and tend to cancel each other. One is the inclusion in placental scar counts and persisting implantation sites that correspond to prenatal losses. This would tend to make the estimate of nestling mortality too high. The second error is that the trend of nestling mortality is interrupted among the young whose mothers make up the samples. This would make the estimate too low.

The exception noted is the apparent decline in nestling mortality in July, 1954, at which time the *Microtus* population was rapidly declining. The reason for such a decrease in mortality is unknown, but this suggests that increased nestling mortality did not contribute to the cyclic decline of the population.

M. californicus. The data on comparative numbers of placental scars and "active" mammae are too limited for this species to show any significant change from sample to sample (Table 15). Nestling mortality, as calculated by this method, is somewhat lower in March and April of 1955, when the population reached peak density, but these calculated figures may not reflect the true situation. The overall minimal loss for this stage of life is estimated as 32%, compared to 38% in *M. montanus*.

Individual parturition and nestling mortality is of considerably greater magnitude than prenatal mortality, and thus may have an important influence on population density. Loss to predators of whole litters

TABLE 15. Parturition and nestling mortality in voles.

<i>Microtus montanus</i> Sampling Date	MEAN NUMBER \pm S. E., AND SAMPLE SIZE (N)		
	Placental Scars, A	"Active" Mammæ, B	A - B = Nestling loss
1953			
June.....	7.00 \pm .45 (5)	4.50 \pm .50 (6)	2.50 \pm .67 36.7%
July.....	5.83 \pm .48 (6)	3.00 \pm 1.16 (5)	2.83 \pm 1.25 48.6%
Sept.....	5.17 \pm .17 (23)	3.58 \pm .18 (20)	1.59 \pm .25 30.8%
1954			
June.....	6.80 \pm .42 (15)	3.50 \pm .28 (15)	3.30 \pm .50 48.6%
July.....	6.00 \pm .71 (5)	5.25 \pm .48 (4)	0.75 \pm .86 12.5%
Sept.....	4.00 \pm .38 (6)	3.80 \pm .20 (5)	0.20 \pm .42 5.0%
<i>Microtus californicus</i>			
1953-54			
Nov.....	3.36 \pm .20 (16)	2.13 \pm .57 (8)	1.23 \pm .60 36.6%
Mar.....	4.80 \pm .73 (5)	3.00 \pm .41 (4)	1.80 \pm .84 37.5%
1954-55			
Nov.....	4.00 (3)	4.00 (1)	0.0
Feb.....	4.50 (2)	3.00 (1)	1.50 33.3%
Mar.....	5.00 \pm .43 (7)	3.75 \pm .25 (4)	1.25 \pm .50 25.0%
Apr.....	4.75 \pm .25 (5)	3.50 \pm .65 (4)	1.25 \pm .70 26.3%
June.....	5.00 \pm .23 (13)	3.17 \pm .23 (12)	1.83 \pm .33 36.6%
July.....	3.40 \pm .40 (5)	2.50 \pm .50 (4)	0.90 \pm .64 26.4%

soon after their birth, or mortality of whole litters due to maternal death prior to the time when the nestlings can be successfully weaned, may further contribute to mortality at this stage. The data for *M. montanus* suggests that increase in individual mortality was probably not the cause of the cyclic population decline that occurred during the summer of 1954. If anything, individual nestling mortality was low during this period, and had a contra-cyclic effect. However, loss of whole nestling litters might have increased greatly during the period of population decline of *M. montanus* and this would have gone undetected.

WEANLING AND EARLY JUVENILE MORTALITY

Once young voles begin to be active outside of the nest, they are exposed to greater risk of predation. If two assumptions are made, a rough estimate of mortality during the period of weaning, when the young voles become active outside of the nest, can be calculated. These assumptions are that the trap line removes most of the trappable mice encountering the line, and that females and young are equally trappable. This second assumption is probably not strictly correct, but if trappability of females and young maintains the same relationship, the mortality esti-

mate based on the assumptions will be valid for comparative purposes. The sum of placental scars in the uteri of females caught is then an index to the number of young born, still subject to the errors discussed in the previous section. If this number is corrected for nestling mortality and compared with the number of young (juvenile and sub-adult classes; see below) caught, the difference may be considered due to the weanling and early juvenile mortality.

M. montanus. The figures on sums of placental scars and the calculated number of weaned young are given in Table 16. The number of young in a sample is not strictly comparable at different times in the breeding season. Early, only juveniles are represented, while later both juveniles and sub-adults are included. This would account for the difference in loss between the June and July samples in 1953, since the older animals in the second sample had been subject to mortality for a longer period.

TABLE 16. Weanling and juvenile mortality in voles.

<i>Microtus montanus</i> Mean Sampling Date	Sum of placental scars in females per sample	Calculated no. of weaned young, A	No. of young in sample, B	A - B = juvenile loss, %
1952 June.....	31	...	20	...
Sept.....	46	...	27	...
1953 June.....	44	28	23	17.9
July.....	85	44	25	43.2
Sept.....	317	219	196	10.5
1954 June.....	158	81	75	7.4
July.....	36	31	17	45.1
Sept.....	20	19	12	36.8
<i>Microtus californicus</i>				
1953 Mar.....	7	...	8	...
Apr.....	7	...	20	...
Nov.....	54	34	7	79
1954 Mar.....	24	15	7	53
Apr.....	0	...	3	...
Nov.....	4	...	0	...
1955 Feb.....	9	6	2	67
Mar.....	35	26	5	82
Apr.....	24	18	11	39
June.....	110	70	79	...
July.....	43	32	24	25

The very low estimated mortality for September, 1953, is significant in this regard, since the sample also included a large proportion of sub-adult animals. This low mortality of young voles is considered the major contribution to the peak population attained at this time. Mortality the following spring also seemed very low, as the June, 1954, sample indicates. Later in the season, however, mortality must have increased enormously, since very few young were present in the fall sample.

M. californicus. A similar calculation of weanling mortality may be made for this species (Table 16), but the figures resulting from such an estimate are not convincing. Weanling mortality seems to range from 0 to 82% (Mar., June, 1955). Sources of error which

TABLE 17. Sex and age distribution of the total¹ catch of *Microtus montanus*.

		1952		1953							1954					Total
		June 24	Sept. 10	May 18	June 11	June 24	July 31	Sept. 6	Sept. 10	Oct. 4	Apr. 30	June 12	June 18	July 11	Sept. 30	
Adults	Number of males	6	10	14	26	8	16	14	8	1	4	22	9	6	2	146
	Number of females	8	17	6	31	12	11	23	22	3	2	14	11	8	6	174
	Number of males per 100 females	75	59	234	81	67	145	61	36	33	200	157	82	75	25	84
Juveniles and sub-adults	Number of males	14	20	0	2	12	13	55	59	14	0	20	18	8	12	247
	Number of females	6	9	0	3	9	11	32	50	14	0	26	9	9	10	188
	Number of males per 100 females	234	222	...	67	133	118	172	118	100	...	77	200	89	120	131
	Per cent of total catch	59	52	0.0	8	51	47	70	79	88	0	56	58	55	73	

¹Excluding animals so mutilated in traps that sex-age class is unknown.²Sample from fertilized meadow.

might produce such distortion are several. The proportion of multiparous females in the samples is somewhat higher in *M. californicus* than in *M. montanus* (Fig. 2), and placental scar counts in such females are subject to more error due to the presence of more than one generation of scars. Furthermore, the lack of synchrony in the onset of breeding activity within the *M. californicus* population is in marked contrast to the almost simultaneous initiation of breeding in *M. montanus*, and this produces a sample in which the clear "mother-young" relationship, on which assumptions the calculations are based, is obscured.

In spite of the above objections, it would seem that in *M. californicus* weanling mortality might have been lower than usual in the April-July, 1955, period, when the population reached a peak density.

POST-WEANLING MORTALITY

Estimation of mortality subsequent to early juvenile life is a difficult problem in microtine rodents, largely because of the lack of sufficiently precise criteria of age, as discussed above.

M. montanus. In 1952, the proportion of young in the catch is about the same in the June and September samples (Table 17). The next year very few young are found until the first litters are weaned, when the proportion abruptly rises. The percentage of young in spring and mid-summer remained at the level found in the 1952 catches, but by September the proportion was significantly higher ($P < .0004$). Thus, the peak population of the autumn of 1953 was mainly due to the large number of young present, although the absolute number of adults compared to the fall of 1952 had increased also. Other evidence points to better adult survival (see above, Correlations with Previous Reproduction), but whereas increase in the adults caught per trap line between fall, 1952, and fall, 1953, was 22% the increase in young was 189%.

In the spring of 1954, there was a significantly greater proportion of young than in June of the preceding year ($P < .001$). This would be expected in

view of the earlier beginning of breeding in 1954. As the season advanced, the proportion of young remained at its usual level, in spite of the great decrease in numbers that was taking place. This, plus the high proportion of young in the September, 1954, catch, suggests that mortality was severe in all age classes. The overall sex ratio in snap-trapped *M. montanus* was 393 ♂♂ : 362 ♀♀. This overall ratio obscures the differences in sex ratio in different age classes and at different seasons. Such differences are a reflection of differential activity, which presumably results in differential mortality for the two sexes. These variations are presented in Table 17.

Two samples of the early breeding population, containing only adults, indicate that many more males than females are caught at this time of year. The males are believed to be more active than the females at this time because of the onset of the breeding season. Increased activity makes them more vulnerable to other, non-artificial types of predation, as well as increasing their trappability. As the breeding season continues, the proportion of adult males declines steadily, with the sole exception of the mid-summer sample in 1953. The decrease in number of males is attributed to continuing high mortality of adult males, and slower recruitment of males, relative to females, from the young of the population. This lower recruitment of males is due to the higher mortality among juvenile and sub-adult males as reflected in the greater numbers of males than females caught in these age classes. As the breeding season draws to a close, the sex differential in mortality apparently disappears among non-breeding individuals, for two post-breeding samples had an equal sex ratio, and in addition were composed largely of immature individuals, indicating that most of the adults of the breeding season just passed had died. However, a few mature individuals may over-winter, as is indicated by the presence of old placental scars in two females of the May, 1953, sample. It is believed that these persisted from the previous fall, instead of representing sporadic winter breeding.

TABLE 18. Sex and age distribution of the total¹ catch of *Microtus californicus*.

		1953					1954					1955							Total
		March 16 April 21 August 17 November 10 November 15					March 21 April 14 June 16 ² August 11 ² November 25					February 14 March 19 April 7 May 12 June 15 July 14 August 10							
Adults	Number of males.....	6	1	2	9	29	5	6	1	7	6	11	11	11	4	2	7	1	119
	Number of females.....	4	8	2	12	32	9	2	11	4	15	6	11	11	2	19	7	8	163
	Number of males per 100 females..	58		100	75	94	100		53	40		184	100		29		53		73
Juveniles and sub-adults	Number of males.....	3	10	13	0	3	5	1	11	4	0	1	2	10	3	47	13	14	140
	Number of females.....	5	10	13	4	0	2	2	15	4	0	1	3	1	3	32	11	16	122
	Number of males per 100 females..	87		100	75		150		79	..		100	300		142		100		115
	Per cent of total catch.....	44	69	87	16	5	33	27	69	42	0	11	18	33	50	79	63	77	

¹Excluding individuals so mutilated in traps that sex-age class is unknown.

²Data from S. F. Cook, Jr.; specimens not seen.

No difference exists between the adult sex ratios in the June and September samples of 1952 and 1953. In 1954, the decline in the ♂ : ♀ ratio progresses more slowly than in the previous years, although the difference between the June samples in 1953 and 1954 is not highly significant ($P = .168$). This greater persistence of males parallels the lower level of reproductive activity at this time, as reflected in pregnancy rate and might be expected if the males were less active.

M. californicus. As was done for the montane vole, certain features of mortality in *M. californicus* may be inferred from the sex and age composition of the samples. These are presented in Table 18. The population which "over-summers" the dry period at the end of the summer, following the cessation of breeding, consists largely of sub-adult individuals born in the preceding breeding season. The sex ratio is about equal. With the appearance of fresh plant growth following the first winter rains, breeding recommences in the exclusively adult population that survived the dry season. The November samples all have more adult females than males. This may be due either to greater activity of the females at this time, or, what is more likely, to higher mortality among the males during the late summer. Later the adult sex ratio generally favors males, but after this, the samples for April, 1953, June, 1954, and June, 1955, indicate that the sex ratio becomes highly female-favored, at a time when the greatest proportion of young are found in the samples. This is interpreted as a higher adult male mortality resulting from greater activity (the early spring samples), leading to a preponderance of adult females later in the season. Among the young produced in this breeding season, the males slightly outnumber the females in the catch. This may be an indication of higher juvenile mortality among the males, which would result in a relatively

faster rate of recruitment of females than males into the class of mature individuals.

This pattern of mortality in the different sex and age groups of the *M. californicus* population resembles in its general features the pattern previously described for *M. montanus*. A higher mortality rate among young male voles, and among adult males at the beginning of the breeding season, is balanced by a higher mortality rate among adult females during the bulk of the breeding season, especially toward the end. Non-breeding populations in both species are composed largely of sub-adults having a 1:1 sex ratio.

SUMMARY: MORTALITY

The primary control of population density in *Microtus montanus* at Sagehen Creek seems to be mediated through the agency of mortality. Prenatal mortality is moderate, although post-implantation loss of whole litters may possibly be heavy. Prenatal mortality was lowest as the population density reached a peak in the fall of 1953, indicating that this may be one of the less important proximate causes of cyclic fluctuations.

Postnatal nestling mortality, while heavy, did not increase during the crash of the vole population, as far as it could be measured. The factor that allowed the population to build up to a peak in 1953 was a low rate of weanling and juvenile mortality. The population crash in 1954, conversely, seemed due to a very high rate of weanling and juvenile mortality. Mortality among adults, especially among those individuals having passed through the previous winter, is normally high in summer. This being the case, rapid recruitment into the older age classes, from among the young born in the summer, is necessary if the population is to be sustained. If annually high mortality among the young results in a failure of recruitment into the older age classes, these classes will decline, and production of young, on a population

basis, will also decline because of the shortage of mature voles. Then declining productivity, plus the high mortality in all age classes, leads to a "crash" decline of the population. Martin (1956:410) recently suggested that a similar mechanism controlled the density of a "non-cyclic" population of *Microtus ochrogaster*.

The available data on *M. californicus* are not adequate to pinpoint the stage at which mortality controls population density. Pre-implantation mortality could not be estimated, but post-implantation losses were small and did not vary in a consistent pattern from year to year. Natality shows no cyclic variation, and the observed changes in litter production are neither large enough nor consistent enough to account for the magnitude of change in population density during the cycle, from peak to crash. This leaves the burden of population control on postnatal mortality, but the stage of the vole's life-cycle that is most sensitive, in terms of cyclic variation in mortality rates, cannot be detected from the data at hand.

DISCUSSION

COMPARATIVE ASPECTS OF REPRODUCTION

A comparison of reproduction during a population cycle in two species of *Microtus* brings out many points of similarity, and also of difference. These similarities and differences must be interpreted in terms of the whole ecology of each species, since the attributes of each species which allow them to persist in radically different environments may be quite different. As was mentioned earlier, the most notable difference between the environments of the two voles is the contrast in climate; the reproduction of the two species will be compared with this in mind.

Correlations with length of breeding season. Reproduction of the two species is compared in Table 19. In the milder climate of Tilden Park, in the Berkeley Hills, the breeding season of the California vole is about twice as long as that of the Sagehen voles, in the Sierra Nevada. Concurrent, and perhaps correlated with this difference in length of breeding season, are other reproductive factors. Thus, during the more prolonged breeding season of *Microtus californicus*, litter size is smaller and precocious breeding is rare. The size of litters in *M. californicus* produced by primiparous females is smaller than that of multiparous females. In contrast, *M. montanus* accomplishes all of its breeding in a short time, and litter size is large, even among primiparous females. In this species, precocious breeding seems common, as is indicated by the lower minimum breeding weights recorded for both sexes. Incidence of post-partum breeding seems to be about the same in both species, and length of gestation is identical.

There is conflicting evidence on the relationship between female size or age and litter size in different species of *Microtus*. In captive *Microtus agrestis* (Leslie & Ranson 1940:36), *M. arvalis* (Rörig & Knoche 1916:359), *M. pennsylvanicus* (Bailey 1924:538; Pooley 1949:317), and *M. oregoni* (Cowan & Arsenault 1954:205), a common pattern was found.

TABLE 19. Comparative reproduction in *Microtus californicus* and *Microtus montanus*.

	<i>M. californicus</i>	<i>M. montanus</i>
Length of breeding season, days.....	270-320	140-155
Litter size, embryos/female...	4.94 4.20 ¹	6.47
Litter size of primiparous females.....	4.61 ± .25 3.91 ± .18 ¹	6.35 ± .22
Litter size of multiparous females.....	5.19 ± .34 4.45 ± .16 ¹	6.55 ± .31
Weight at maturity (g): males.....	35-40	35
females.....	25-30	33
Minimum weight recorded (g): breeding males.....	33.4	25.0
pregnant females.....	25.0	19.5
Incidence of post-partum breeding, per cent.....	30	24
Length of gestation, days ²	21	21

¹From Greenwald, 1957. The salt marsh edge inhabited by this population is moderated by more fog, and by a constant source of green vegetation (*Salicornia*) in contrast to the more severe late summer desiccation of Tilden Park grassland. Because of these factors, the salt marsh population may have a longer breeding season than that of the upland grassland, but this is unproven.

²From Hatfield, 1935.

Litter size increases for the first two or more litters produced by a female, but begins to decline after the fourth or fifth litter (second in the case of *M. arvalis*). In contrast to this situation, there is a direct correlation between female weight (~age) and litter size in wild-caught *M. arvalis* (Naumov 1936:149). The difference between laboratory and field data may be due to the scarcity, in natural populations, of old females corresponding to the captive age group which has already produced several litters. An alternative explanation is that weight may not show sufficient direct correlation with age in this species for the age-litter size correlation to be valid (see also Frank 1956:52 ff.).

M. montanus is the only microtine so far recorded in which the litter size of primiparous females is not significantly smaller than that of multiparous females. There is, however, incomplete evidence suggesting the same phenomenon in *Dicrostonyx groenlandicus* (Manning 1954:39-40) and perhaps in a race of *M. oeconomus* (Bauer 1953:89). Howell (1924:989) reports a sample of 19 pregnant *M. montanus* in which the number of embryos in the 9 heaviest females averaged 6.2, as compared with a mean of 4.9 embryos for the 9 lightest females. He considers this difference to be related to age, but it is more probably fortuitous. A similar comparison of the present material gives an average of 7.0 embryos for the heaviest females, and 5.8 for the lightest but this is not significant ($P = .23$); as already mentioned (see Correlations with Previous Reproduction), no significant difference exists between litter sizes of primiparous and multiparous females and

there is no real correlation between litter size and weight.

Another unique feature is that whereas in *M. montanus* males and females mature at about the same age, as determined by their size, in *M. californicus* (also Greenwald 1957:425, 435), *M. pennsylvanicus* (Hamilton 1941:7), *M. agrestis* (Leslie & Ranson 1940:33), and *M. oregoni* (Cowan & Arsenault 1954:202), females mature more quickly than males.

The significance of this inverse relationship between length of breeding season and intensity of reproductive effort might be that, if enough young are produced during a short breeding season, the mortality inevitable during the non-breeding season may be balanced. When the breeding season is longer, the rate of production may thus be correspondingly less, and the necessary annual production of young will still be attained. Lack (1954:143) has objected to this teleological interpretation, on the grounds that "reproductive rate is a product of evolution, and . . . the number [of young in a litter] . . . should be that which results in the maximum number of surviving offspring. . . ." He suggests that clutch size in birds and litter size in mammals are limited by the number of young that the parents can feed. Litters above-normal in size produce fewer survivors than litters of normal size, so that selection produces a certain optimum litter size.

Lack's emphasis is on the availability of food as the main determiner of nestling survival, and hence of clutch or litter size. However, food is rarely limiting in quantity to the grazing voles in the same sense that insect supplies may be limiting to the small passerine birds from which Lack draws most of his examples. Hence, his theory does not seem to explain the differences in litter size that are found in *M. montanus* and *M. californicus*.

In certain respects the difference in vole litter size is similar to that found in many birds, in which populations of more northern distribution have a shorter breeding season and larger clutch size than populations of the same or closely related species to the south (Lack 1947:303 ff.). Lack attributed this to the longer hours of daylight in the north which allow the birds to spend more time foraging than their relatives in the south (*op. cit.*:319). This has the effect of increasing the food supply for the nestlings. In the case of the two microtine species studied, Lack's explanation will not suffice because they live in the same latitude, the "north-south" effect being accomplished by altitudinal difference. Furthermore, voles are not dependent on daylight hours for feeding. Increase in clutch size with increasing altitude has also been reported for song sparrows (*Melospiza melodia*) in California (Johnston 1954:270).

Other microtines exhibit an inverse relationship between litter size and length of the breeding season, regardless of food conditions (Table 20). While it should be realized that length of the breeding season varies in different years, a general correlation is apparent. *M. oregoni* forms an interesting deviation

in that its average litter size is the smallest recorded for a microtine, yet the length of the breeding season is intermediate. Its habits also deviate from the usual microtine pattern in that it is semi-fossorial, and thus presumably less exposed to predation mortality than surface-dwelling species of *Microtus*. In these habits it most closely resembles *Pitymys nemoralis*, having a litter size of 2-3, usually 2 (Glass 1949:72), and *P. pinetorum*, which has 2-4 young per litter (Hamilton 1938:167; Benton 1955:56).

A somewhat different correlation, between litter size and latitude, but not, apparently, length of breeding season, is tabulated for snowshoe hares by Rowan & Keith (1956:278).

Seasonal variability in reproduction. Also related to climatic differences between the two study areas is the pattern of seasonal change in litter size and reproductive effort. In *M. californicus*, litter size is low at the beginning of the breeding season (late fall), and members of the population do not come into breeding condition simultaneously, but rather over a considerable period of time. Litter size then rises to a maximum, and declines in the last part of the season. In *M. montanus*, on the other hand, litter size is maximum at the beginning of the breeding season, and then declines progressively. Initiation of breeding in all members of the population seems to be practically simultaneous.

Lack (1954:146) cites several cases in birds that are analogous to the situation in the two microtines. In the great tit (*Parus major*) at Oxford average clutch size declines steadily as the season progresses. In other double- or treble-brooded species, clutch size rises from early April to early June and then declines. Quantity of food available for feeding of young is believed by Lack to correlate with these seasonal variations. Voles differ from birds in this respect, as previously mentioned. However, while forage may be available in quantity for voles, food quality varies seasonally and this shows a correlation with litter size in both species of *Microtus*.

Variation in food quality. The food habits of *Microtus* are not simple. Voles eat a variety of green plant parts, and their diet probably includes at one time or another all species of the plants within their habitat. In the meadows along Sagehen Creek, a large proportion, estimated at about 90%, of the vegetation consists of several species of *Carex* and *Juncus*. Observations indicated that these plants were very frequent as cuttings in the vole runways, and it is presumed that for *M. montanus* they form the major part of the diet.

Beginning in June, 1953, samples of *Carex* were collected at intervals throughout the following two summers. These were analyzed for crude protein content by the Kjeldahl method, and the results are plotted in Fig. 6. This graph shows that there is an initial peak, and subsequent decline, in ovulation rate, litter size and protein content of food in *M. montanus*. For the common annual grasses in the Tilden Park area, no analyses are available for a comparison of

TABLE 20. Relationship between litter size and length of breeding season in *Microtus*.

Species	Approximate length of breeding season ¹	Litter size	Locality	Latitude	Altitude	Authority
<i>Microtus miurus</i>	90 days	8.23	Arctic Slope	71° N.	400 to	Bee and Hall, 1956
<i>M. oeconomus</i>	90	7.5	Northern Alaska		3,000 ft.	
<i>M. montanus</i>	150	6.47	Sagehen Creek, Calif.	39° N.	6,600 ft.	present study
<i>M. pennsylvanicus</i> ..	200	5.07	Ithaca, New York	42° N.	400 ft. ?	Hamilton, 1937a, 1941
	See note ²	5.94 ²	Glacier Nat. Park, Mont.	49° N.	3,700 ft.	P. L. Wright unpublished data
	See note ²	4.60 ²	Nat. Bison Range, Mont.	48° N.	3,100 ft.	
<i>M. californicus</i>	280	4.94	Tilden Park, Calif.	38° N.	1,000 ft.	present study
	>280?	4.20	San Rafael, Calif.	38° N.	10 ft.	Greenwald, 1957
<i>M. ochrogaster</i>	300	3.4	Lawrence, Kansas	39° N.	800 ft. ?	Jameson, 1947
<i>M. oregoni</i>	240	2.95	Vancouver, Brit. Col.	49° N.	near sea level?	Cowan and Arsenault, 1954
<i>M. oeconomus</i>	<120 ³	7.50 ⁴	Rosta, Norway	69° N.	400 ft.	Hoyte, 1955
	150	5.80 ⁴ 5.44 ⁴	Øyer, Norway Eidfjord, Norway	61° N. 60° N.	3,300 ft. 3,800 ft.	Wildhagen, 1953
<i>M. agrestis</i>	195	5.0	Caernarvonshire and Anglesey, Wales	53° N.	near sea level?	Brambell and Hall, 1939

¹Refers only to the period of major breeding effort and does not include occasional breeding which may occur in some individuals when the majority of the population is not breeding. Thus winter breeding in *M. pennsylvanicus* and *M. agrestis*, and the late summer breeding in *M. californicus* and *M. ochrogaster* are excluded. More extensive winter breeding may occur in the arctic (*M. oeconomus* and *M. miurus*), but this is not well documented.

²Length of breeding season is not adequately known, but is considerably shorter in Glacier Park than on the Bison Range. Litter size is calculated for July samples only (4 years). The difference is highly significant ($P < .001$).

³A more definite figure cannot be calculated from the data given, but length of the season is known to be shorter in northern Norway than in areas 500-600 miles further south studied by Wildhagen.

⁴Calculated from July and August samples only. The difference between Hoyte's and Wildhagen's means is "probably significant" (Hoyte).

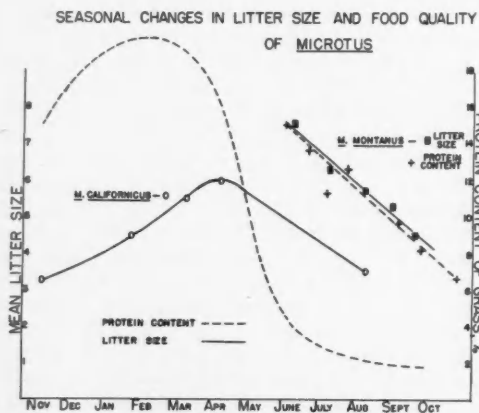


FIG. 6. Seasonal variation in litter size and food quality in *M. montanus* and *M. californicus*, showing direct correlation between litter size and crude protein content of common grasses in the habitat of each species. Litter size of both species, and protein content of *M. montanus* food, based on data from present study. Protein content of *M. californicus* food based on various sources (see text).

their nutritive quality with the peak of litter size in *M. californicus*, but there is some indirect evidence. Sampson & McCarty (1930:71) studied the growth of

the perennial grass *Stipa pulchra* in the Berkeley area and found that the period of most rapid growth occurred in May. They also note that the annual grasses in this area matured earlier than *Stipa*, presumably in March or April. It is known that highest protein content and general high level of nutritive value associated with it occurs in the plants undergoing succulent stages of early growth (Campbell & Cassady 1954:41). Bonner (1950:308, 310), citing the work of Gregory & Sen (1937), says that "protein nitrogen level in barley . . . varies . . . from 3.23% in the youngest leaves to 4.06% in a mature leaf and 2.52% in the oldest leaves." This being the case, the nutritive value for *Microtus* foods in Tilden Park must increase or at least be maintained until March or April, through the period of rapid growth that follows the depressed growth in the winter. During the period of depressed winter growth, there is only a slow increment to leafage of the new grass available to the voles, so that in addition to the lower protein content of the youngest leaves, the quantity of food of a high qualitative grade is restricted, in contrast to the abundance of new growth available to *M. montanus* at the beginning of the breeding season.

Thus the quality of the total diet of *M. californicus* probably is low at the onset of breeding in the fall, and gradually improves as more new grass becomes

available. Gordon & Sampson (1939:17 ff.) have shown that after the early growth period, protein content declines in grasses in the southern San Joaquin Valley, and this decline must also occur in the grasses in Tilden Park following maturity. From these evidences, it is concluded that there is a direct correlation between food quality and litter size in *M. californicus* as well as in *M. montanus*, as illustrated in Fig. 6.

Naumov (1936:151) also found seasonal natality changes in *M. arvalis*, there being a decrease in litter size later in the season, which he attributed to decrease in food quality caused by drought, although he had made no chemical analyses. Biswell, Taber, Hedrick, & Schultz (1952:460 ff.) and Taber (1953:183) found that the average number of fetuses per doe in the black-tailed deer (*Odocoileus hemionus columbianus*) also varied directly with nutritional quality of browse available to them in Lake County, California. They concluded that "the difference in nutritional planes is probably based on adequacy of assimilable protein and phosphorus . . ." in the different cover types (1952:463). Cheatum & Severinghaus (1950) record similar findings for the white-tailed deer (*O. virginianus*) in New York.

That nutrition may have a pronounced effect on the number of young borne by a female has long been known in the case of domestic (including laboratory) animals. Marshall (1922:633 ff.) describes the process called "flushing," long practiced on Scottish sheep, in which the number of lambs produced in a flock is increased by providing the ewes with "additional food at the tupping [breeding] time and for about three weeks previously, while maintaining them upon grass only during the greater part of the year." Slonaker & Card (1923), to select only one case, have demonstrated the importance of nutrition in determining the litter size of laboratory rats.

With two exceptions, other species of *Microtus* that have been studied with regard to seasonal changes in litter size show a pattern comparable to that described for *M. californicus* (see Hamilton 1937a:785; Jameson 1947:146; Cowan & Arsenault 1954:206). Conflicting and incomplete evidence exists for *M. arvalis*. In Germany and Russia this species may show a progressive rise in litter size to a peak, and then a subsequent decline (Stein 1952:18; 1953:542; Frank 1956:51, 55 ff.; Maximov 1948). Other data from these countries suggest that litter size may be maximal at the start of the breeding season in some situations (Rörig & Knoche 1916:352; Naumov 1936:151; Stroganova 1954:71 ff.). If this is true, *M. arvalis* at times may possess a pattern of seasonal change in litter size similar to that of *M. montanus*.

Bee & Hall (1956:133) report that in *M. oeconomus* in Alaska, the number of embryos per female "gradually decreases from an average of 7.8 in late June to 5.0 in late August." Litter size in the brown lemming (*Lemmus trimucronatus*) also followed the same pattern: a maximum at the beginning of spring

breeding, followed by a steady decline until breeding terminated in the fall (*op. cit.*: 94-96).

COMPARATIVE ASPECTS OF MORTALITY

The pattern of mortality among sex and age classes does not appear to vary significantly among the several microtine species thus far studied. This pattern was described above for *M. montanus* and *M. californicus*, and will be summarized briefly.

Adults. The pre-breeding population consists of adults that entered the non-breeding season as juveniles or sub-adults, and have now matured. Males are most active at this time, and suffer heavier mortality than the females, thus leading to a sex ratio which is increasingly female-favored as breeding continues.

Rörig & Knoche (1916:361), Naumov (1936:156) and Fenyuk & Sheikina (1940) also found this to be the case in *M. arvalis*. The Russian workers employed a technique which presumably captured all voles within the area sampled; Naumov dug out all voles within a circular area of 0.5 hectares, and Fenyuk & Sheikina live-trapped in three small straw-stacks only. Thus they regard their samples as completely representative of the population in terms of sex and age ratios. The fact that the mortality trends calculated from these representative samples and the trends inferred from snap-trapped samples agree lends confidence to results from snap-trapping.

Bee & Hall (1956:134, 151) interpret a summer shift in adult sex ratio to the favor of females in *M. oeconomus* and *M. miurus* in the same way, attributing it to greater exposure of the males to predation.

As breeding declines later in the season, adult females suffer increasing mortality, until at the end of the breeding season, almost all of the adult males and most of the females are dead. The population which then enters the non-breeding season is composed almost entirely of individuals born during the breeding season just past. This phenomenon of an "annual" population in mammals was first noted by Baker & Ranson (1933:488) for *M. agrestis*, and subsequent work revealed the same situation in *M. arvalis* (Naumov 1936:161), *M. pennsylvanicus* (Hamilton 1937b:505), *M. ochrogaster* (Jameson 1947:147), *M. guentheri* (Bodenheimer 1949:54), and *M. oregoni* (Cowan & Arsenault 1954:207).

Mortality during the non-breeding season is related to the size of the population which enters this period, in *M. montanus* and *M. californicus*. This is inferred from the similarity in numbers caught in any year at the end of the non-breeding season. It suggests a "carrying capacity" phenomenon (Leopold 1933:51) for the habitat of both species. Several of Hamilton's graphs of *M. pennsylvanicus* population trends (1937a:782) might also lend themselves to a "carrying capacity" interpretation. Also, Chitty (1952:536) found little difference in pre-breeding densities of *M. agrestis* in the springs of 1937 and 1938.

Young. In both *M. montanus* and *M. californicus*, mortality in the juvenile and sub-adult age classes during the breeding season is interpreted to be higher

among males than among females. The same inference may be drawn from Naumov's (1936:156) data, although he does not specifically discuss it. Higher juvenile male mortality would result in a relative rate of recruitment from the sub-adult into the adult age group lower for males than for females during the breeding season. This process would then contribute to the maintenance of the female-favored sex ratio among adults that was established by the adult differential-sex mortality early in the breeding season. This pattern of mortality in voles may be generalized in a family of schematic survivorship curves (Fig. 7).

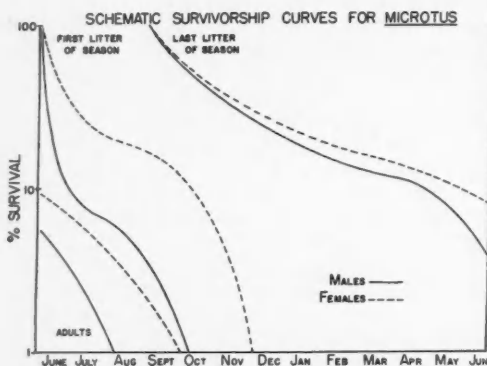


FIG. 7. Schematic survivorship curves for summer-breeding voles (*Microtus*). Litters born between first and last litters of the season are assumed to be intermediate in survival rates. Assumption of age-specific mortality is based mainly on Naumov (1936) and Fen'yuk & Sheikina (1940).

CYCLIC ASPECTS OF REPRODUCTION

Litter Size. As already noted, Hamilton (1937a:784) found that in *M. pennsylvanicus* there was a change in litter size corresponding to the stage of the cycle, with progressively larger litters occurring as the population built up to a peak, and then a sharp decline in litter size as the population crashed. This was not found in either Californian species. Instead, the reduction in ovulation rate and litter size with increasing population density may be interpreted as an intercompensatory "inversivity" response to population density (Errington 1946). The continued depression of ovulation rate and litter size in *M. montanus* during the period of decreasing population density may, however, be due to some sort of "cyclic" factor, either intrinsic or extrinsic to the population. This lowered natality is not known to occur in *M. californicus*, because a crash decline of population has not been studied in this species. Lower litter size, then, may contribute to the decrease in population density during the "decrease" phase of a microtine cycle, but the rapid and extreme decline in density is of too great a magnitude for lowered natality to be considered as anything more than a secondary factor correlated with the cyclic decline.

Prevalence of pregnancy. Hamilton (1937a:783)

also claims an acceleration of the breeding rate in *M. pennsylvanicus* as the population increased. The index of breeding rate he used was the prevalence of post-partum breeding in the population. No significant change in this was noted in *M. montanus* or *M. californicus*, although the samples are small. Prevalence of pregnancy, which would seem to be a better index of breeding rate, was inversely related to population density.

Hamilton ascribed the direct relationship between breeding rate and density in *M. pennsylvanicus* to the decreased chance of an estrous female meeting a fertile male during periods of low population. Greenwood (1956:221) points out that in the case of *M. californicus*, which is an induced ovulator, this relationship would be much less important in affecting breeding rate than in the case of a spontaneously ovulating species because post-partum estrous may last for days, and a male is thus much more likely to be encountered. Errington (1946:153) is also critical of Hamilton's interpretation of breeding rates, and points out that a high breeding rate was maintained after the population of *M. pennsylvanicus* had suffered a severe decline. Similarly, Elton, Davis & Findlay (1935:283) found that the reproductive rate in *M. agrestis* was not affected during a cyclic decline, and Chitty (1952:519) found that "lowered fertility was not invariably associated with a decline in numbers" in the same species. In a third study of *M. agrestis* by Godfrey (1955:212), breeding occurred on both study areas during the year of the crash.

Length of breeding season. Finally, Hamilton (*op. cit.*:785) reports that the breeding season is longer as population density increases. In *M. californicus* the breeding season was longer in 1953-54 when a minor peak in populations occurred. On the other hand, the season was shortened in 1954-55, when the major cyclic peak was attained. Furthermore, there was no prolongation of breeding as the peak was approached in *M. montanus*; if anything, breeding was cut short in the fall of 1953 as peak densities were attained. This is paralleled by Piper's (1909:304) account of inhibited reproduction in the same species during a high population density in Nevada. In the *M. agrestis* populations studied by Chitty (*loc. cit.*), breeding stopped in August, 1937, in those areas which reached a peak in the fall of 1937, but continued to October, 1938, in those areas in which the peak was reached in 1938. Thus, there may be two distinct relationships between population density and length of the breeding season in different species of *Microtus*, first, a peak population may be preceded by a prolonged breeding season, and second, a peak population may follow from an unchanged, or even a shortened, breeding season.

CYCLIC ASPECTS OF MORTALITY

The single most important factor in determining whether the *Microtus* populations studied would reach moderate, very high, or very low density following the breeding effort in any given year was the survival of

individuals born during that breeding season. This conclusion applies to *M. montanus*, and very probably also to *M. californicus*. The pre-breeding population in any year is not significantly different, and the reproductive effort during the breeding season in any year changes only slightly, so that the major shift in the two opposing population forces must occur in mortality rates. Prenatal mortality appears to reflect this in that over-all losses at this stage in *M. montanus* were lower in July and September, 1953, than in July and September, 1952 or 1954. However, the greatest difference between the various years seems, from the evidence of age structure, to be in weanling and juvenile mortality. This is evidenced by the very high proportion of young and sub-adult *Microtus montanus* found in the peak population (autumn, 1953). In the *M. californicus* population, on the other hand, survival in all age classes may be equally improved during the population increase, since the proportion of young was no larger in peak populations. It should be realized, however, that the problem of distinguishing adult from sub-adult and juvenile voles seems to be more difficult in *M. californicus* than in *M. montanus*, so that differential survival of an age class in any year might not be so readily detected.

The role of unusually heavy mortality in bringing about a cyclic "crash" has been recognized in other vole populations. Elton, Davis & Findlay (1935:283) and Chitty (1952:534) ascribed declines in *M. agrestis* to excessive juvenile mortality in the spring. Chitty found the decline occurring between January and June, a period when the population consisted mainly of animals born in the last part of the previous breeding season. This excessive mortality was prolonged over at least two generations. Godfrey (1955:212) specifies the late weaning or post-weaning stage as that in which cyclic juvenile mortality is most severe. This corresponds to findings of the present study.

Symptoms of cyclic mortality: stress. Certain symptoms have been described as characteristic of "crash mortality" in mammals, and Christian (1950) was led to the conclusion that these symptoms were all an expression of the "general adaptation syndrome" described by Selye (1946). This theoretical mechanism for the die-off terminating a population cycle was as follows:

A peak in numbers is attained in the autumn, and a population of high density enters into the winter. Winter is considered to be a "period of relative food scarcity, cold, and other severe climatic stresses . . ." (op. cit.:251). High population levels during this unfavorable season produce abnormally severe stress through the action of food scarcity, lack of cover, and fighting among individuals. Physiologically, the reaction to such stress is increased secretion of adrenocorticotrophic hormone from the anterior pituitary, which results in hypertrophy of the adrenal cortex, in an "effort" to provide resistance to the stress. Thus, Christian envisages a "population under highly stressed conditions and undoubtedly taxing its adrenopituitary system to the maximum" (op. cit.:252) in

early winter. At this time, day length begins to increase, and the anterior pituitary responds by secreting gonadotrophic hormones. This places "increased demands on the pituitary at a time when it is already maximally stimulated to produce adrenocorticotrophic hormone in response to stress" (op. cit.:252), and gonadotrophic activity proceeds at the expense of adrenotrophic activity. By early spring the physiological stress of actual reproduction is added, and exhaustion of the adreno-pituitary mechanism is assured. When this exhaustion phase is reached a period of cyclic mortality ensues, and the population crashes.

Several criticisms may be directed at this theoretical mechanism. Christian assumes that winter is inherently the season of greatest stress for cyclic species. However, this is almost certainly not the case for many species of *Microtus*. Food does not suddenly become more scarce during the winter, as opposed to the autumn. A progressive diminution of food supplies may occur in the course of a winter as vegetation is eaten but does not grow, but there is generally a fair vegetative cover in early winter, during which the stress is supposed to develop. Furthermore, many species of microtines store food during the summer, and draw on these caches in the winter (Bailey 1920:71; Criddle 1926:197). Lack of cover is no problem at all to species such as *M. montanus*, since a snow blanket is present throughout most of the winter. In those areas where snow is not persistent, cover and food conditions go hand in hand, and it is still true that there is no sudden deterioration in the transition from autumn to winter. Finally, Christian cites the climatic stress of the winter period. However, Pruitt (1953:33 ff.) has shown that the niche inhabited by most microtines during the winter, that of the ground beneath the snow blanket, has a remarkably stable and relatively warm microclimate. By comparison with winter, the early spring season is much more stressful in terms of weather, food and cover for voles at Sagehen Creek (see also Sviridenko 1934; Craighead & Craighead 1950:217; 1956:147, 298 ff.; Bee & Hall 1956:77).

A more serious objection to the "stress" theory of cyclic decline is that the crash of the population should always occur in the late winter-early spring period. That this is not so is illustrated by the crash of *M. montanus* during the present study, which took place in the late spring and summer (see also Braestrup 1941:48 ff.; Blair 1948:404). Furthermore, mature individuals that have over-wintered should be the most severely affected by the postulated mechanism. Actually, the young born during the breeding season following the autumn peak are the ones that suffer abnormal mortality during a cyclic decline, as shown in the present study and in others cited above.

The portion of the theoretical mechanism that gives rise to most of the above objections is that involving early-winter stimuli eliciting gonadotrophic activity, which increases the pituitary load at a time when stress is supposed to be maximal. If this portion is

eliminated, the factor of overcrowding in the peak population remains, in which stress due to overcrowding inhibits reproduction, as was seen in both vole populations studied. That overcrowding can inhibit reproduction in small rodents is now well established experimentally (Crew & Mirskaia 1931:244; Retzlaff 1938:243; Strecker & Emlen 1953:381; Clarke 1955:76; Southwick 1955:221). Other work (Calhoun 1949:335; Strecker & Emlen *op. cit.*: 380; Clarke *op. cit.*: 80; Southwick *loc. cit.*; Louch 1956:706) indicates that overcrowding may in addition adversely affect juvenile survival.

SUMMARY

The relationship between reproduction and mortality in two species of voles (*Microtus montanus* and *M. californicus*) was studied during a "cyclic" fluctuation in population density of each species. Both species exhibited a generally inverse relationship between natality, as measured by ovulation rate and litter size, and population density. Thus, when density increased, ovulation rate and litter size were reduced, and this decline in natality tended to stabilize the population and "damp" the cyclic increase in vole numbers. Contrary statements, indicating a larger litter size during the period of peak vole densities, have been published. During the "decrease" phase of the cycle, natality in *M. montanus* seemed to remain low, in this way hastening the decline in population density; this agrees with published observation made on *M. pennsylvanicus*.

In contrast to the variation in natality, speed of attainment of reproductive maturity and the prevalence of post-partum breeding were rather constant and independent of the stage of the population cycle. In *M. montanus*, duration of the breeding season also was quite constant, but in *M. californicus* the breeding season, and consequently litter production, varied considerably from year to year. That this variability was not of prime importance in controlling the course of the population cycle in *M. californicus* was shown by the peak population density of 1955, which was attained during the shortest of the breeding seasons. Some earlier studies of vole cycles suggested that the "breeding rate" accelerated, and breeding season was lengthened, during the build-up to peak populations, and that breeding was then curtailed during and following the "crash." The present study, and other earlier studies as well, do not support this interpretation.

Since the variation observed in reproduction was relatively minor, mortality must then be the variable that produced the differences in the vole populations from year to year. The population of adult voles at the beginning of breeding differed only moderately between successive years prior to the "crash" decline. The density that the population attained at the end of each breeding season depended upon the survival of individuals born during that breeding season.

Prenatal mortality in *M. montanus* was lowest in the summer and autumn of 1953, when the population

reached peak level. It increased sharply during the population decline the next year. Prenatal mortality could not be estimated accurately for *M. californicus*, but it seemed to be of the same order as for *M. montanus*, 5-10%.

Postnatal nestling mortality was estimated to be much higher, usually between 30-35% for both species. Although considerable variation in nestling loss was found, it could not be identified as the cause of the excessive mortality occurring in cyclic declines.

The changes in inferred survival of weanling and juvenile *M. montanus* are considered to be the main cause of the differences in population density found in the autumn of the different years. Low mortality in young voles during the breeding season of 1953 resulted in a peak population. Very high mortality the next year seemed to have produced the "crash" decline. Crash declines in other vole populations have also been attributed to excessive juvenile mortality. In *M. californicus* the cause of population peaks and declines may be somewhat different in that survival of all age classes may be equally improved in a peak year, rather than just among the young. However, this is not certain.

The cause of the unusually heavy mortality which terminates the peak of a vole population cycle has been laid to a break-down of the adreno-pituitary system in stressed individuals in the peak population. According to this theory, the crash should occur in the late winter or early spring; actually it occurred in mid-summer in *M. montanus*. Furthermore, overwintering adults from the peak population of the previous fall might be expected to suffer the greatest mortality; actually the juvenile descendants of these adults were the least viable.

Incidental to the work on population cycles, certain basic aspects of comparative reproduction have been uncovered. In *M. californicus*, a vole with a very long breeding season, litter size was moderate and precocious breeding was rare. In contrast, *M. montanus*, which has a very short breeding season, had large litters and precocious breeding was common.

Another difference between the two species is that litter size was largest at the start of the breeding season in *M. montanus*, and then progressively declines. In *M. californicus*, litter size was low at first, rose to a peak in the middle of the breeding season, and then declined again. These patterns correlate with changes in the quality of forage available to the voles. Protein content of grasses in the mountain meadows was highest in early June, when *M. montanus* produced its first litters of the season, and declined through the summer. On lowland, summer-dry hills, grass with the highest protein content was available in April, and was probably of poorer quality both early and late in the breeding season.

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